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# ILLINOIS BIOLOGICAL MONOGRAPHS

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1926

EDITORIAL COMMITTEE

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STEPHEN ALFRED FORBES

WILLIAM TRELEASE

HENRY BALDWIN WARD

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# STUDIES ON THE AVIAN SPECIES OF THE CESTODE FAMILY HYMENOLEPIDIDAE

WITH 9 PLATES AND 2 TEXTFIGURES

BY  
ROY LEWIS MAYHEW

Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward  
No. 260



# **THESIS**

**SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE  
SCHOOL OF THE UNIVERSITY OF ILLINOIS**

**1924**

# NATURAL HISTORY

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## INTRODUCTION

The internal parasites of American birds are little understood, and it was with the idea of finding out something about the species of cestodes and extent of the infections that the investigations herein reported were undertaken. A considerable quantity of material was obtained from the collection of Professor H. B. Ward, who very kindly allowed me to use it. In order to augment this and to secure fresh material, the examination of as large a number of additional hosts as possible was undertaken. While attending the session of the University of Washington Biological Station in the summer of 1923, 45 birds obtained in the region of Friday Harbor, Washington, were examined. A total of 537 hosts has been examined. There were 60 different species among these, and of this number 40 were found to be infected with cestodes. More than half of the specimens of 31 of the species were found to be infected. Since a comparatively small number of some of the host species was obtained, a further analysis of the records would be of little value at present.

As mounts were prepared for a preliminary determination, it was observed that a considerable number of species belonging to the genus *Hymenolepis* Weinland 1858 had been obtained, and they were accordingly brought together for further study. That a comparative study of the family Hymenolepididae, and especially of the genus *Hymenolepis* would be an important contribution to the existing knowledge of this group, was evidenced by an examination of the literature. The numerous papers examined disclosed descriptions of about 160 species which had been assigned to the genus *Hymenolepis*, and that, beyond the comparisons made by Fuhrmann, Cohn, Clerc, and Wolffhügel, no extensive comparative study of the genus had been undertaken. The conclusions herein set forth are the result of a detailed study largely from the literature of each of the species assigned to the genus *Hymenolepis*, and of the twelve new species of which material has been obtained. But five North American species have been reported exclusive of those imperfectly described by Leidy (1887).

I wish to express my appreciation for the very helpful suggestions which Professor Ward has given during the progress of the work, for the use of his extensive library, and for the loan of specimens from his collection. Thanks are due to Professor Frank Smith for the identification of a number of the hosts, and to Professor T. C. Frye, Director of the University of Washington Marine Station, for his interest and assistance in securing the hosts for examination at Friday Harbor, Washington.

## METHODS OF TECHNIQUE

At the beginning a number of killing fluids were tried, with the uniform result that acid fluids, such as Gilson's and Petrunkevitch, react with the calcareous bodies with such violence that large cavities resulted in the preserved worm or the proglottids are puffed out balloon-like by the gas formed within. The most satisfactory killing fluid was found to be a saturated solution of corrosive sublimate in distilled water. This is allowed to act from one to two hours, and replaced by 50 per cent alcohol for one hour, then 70 and 85 per cent alcohol. Great care must be exercised to extract all the corrosive sublimate before staining and mounting, as it interferes with clearing. An effort should be made to secure the worms as fully extended as possible, which may be done by gently pulling them with the fingers protected by rubber gloves or by Looss' (1901) shaking method.

The stain used for toto mounts and sections was in most cases Ehrlich's acid hematoxylin, although Delafield's and Conklin's modified hematoxylin were also about equally satisfactory. The procedure followed was to use Ehrlich's acid hematoxylin full strength, staining in toto for two to four days depending on the size of the worms, rinse off the stain with 50 per cent alcohol, and destain in 10 per cent HCl. The length of time to be allowed for destaining varies with the size of the specimen and can only be determined by practice, but usually only a few seconds or one minute is necessary. The acid is neutralized by a saturated solution of  $\text{Na}_2\text{CO}_3$  in 70 per cent alcohol. The stain is improved by allowing the stock solution to concentrate through evaporation down to a very dark color and this may be used over and over by first filtering to insure the removal of any sediment. The object of the process was to get the largest amount of stain possible into the internal organs, and then to remove as much as possible from the overlying tissues which retain it less strongly than do the reproductive organs. Specimens stained and prepared in this manner were cleared, the desired number of proglottids removed from the selected regions for sectioning and the remainder mounted as tolos. Specimens to be sectioned should not have quite as much stain removed as those for toto mounts, but the remaining pieces may be further destained for mounting as tolos if found to contain too much. Sections thus stained and sectioned may be counterstained with eosin. The counterstain gives the most satisfactory results if rather heavy since the ducts, as vasa deferentia, take it up readily, and, unless too heavy, it does not obscure the other structures. A small outline of the pieces of the cestodes from which proglottids had been removed for sectioning was found very useful. These are conveniently made on small cards the size of the slides, and may be placed behind the slides in the boxes. They are useful also for recording data as to length, width, etc., as well as to show readily the position of the portions sectioned.

## HISTORICAL ACCOUNT OF THE FAMILY HYMENOLEPIDIDAE

The name Hymenolepididae was first used by Ariola (1899), and he defines the genus as follows: "con corpo di media o minima grandezza, e scolice armato di una o piu corone di piccoli uncini." There is no list of genera or discussion of its limits. The name Hymenolepididae was used by Railliet and Henry (1909) and is synonymous with Hymenolepidae, Echinocotylidae, and Dilepinidae, according to Ransom (1909) who gives the following diagnosis:

"Taenioidea: Scolex with an armed rostellum, or without rostellum. Hooks on the rostellum not hammer-shaped. Suckers usually unarmed. A single, or rarely, a double, set of reproductive organs in each segment. Genital pores marginal and bilateral, unilateral, or regularly or irregularly alternate. Eggs with thin transparent shells. Adults in mammals, birds, reptiles, and Amphibia."

Under this family he includes the following subfamilies and genera:

## Dipylidiinae Stiles 1896

Dilepis Weinland 1858	Cyclusteria Fuhrmann 1901
Trichocephaloides Sinitzin 1896	Laterotaenia Fuhrmann 1906
Lateriporus Fuhrmann 1907	Proorchida Fuhrmann 1907
Choanotaenia Railliet 1896	Cyclorchida Fuhrmann 1907
Monopylidium Fuhrmann 1899	Gryporhynchus Nordmann 1832
Anomotaenia Cohn 1900	Angularia Clerc 1906
Amoebotaenia Cohn 1899	Catenotaenia Janicki 1904
Liga Weinland 1857	Dipylidium Leuckart 1863
Leptotaenia Cohn 1901	Oochoristica Lühe 1898
Parvirostrum Fuhrmann 1907	Pancerina Fuhrmann 1899

## Paruterininae

Paruterina Fuhrmann 1906	Metroliasthes Ransom 1900
Culcitella Fuhrmann 1906	Biuterina Fuhrmann 1902
Rhabdometra Kholodkovski 1906	Nematotaenia Lühe 1899
Anonchotaenia Cohn 1900	Stilesia Railliet 1893

## Hymenolepidinae

Oligorchis Fuhrmann 1906	Diorchis Clerc 1903
Hymenolepis Weinland 1858	Haploparaxis Clerc 1903
Subgenus Hymenolepis Weinland 1858	
Subgenus Echinocotyle Blanchard 1891	

The above list gives some idea of the size of the group. That it is a poorly defined group is indicated by the lack of any statement of well marked characters in the family diagnosis. It is best to consider briefly the scolex and its hooks in a few genera in order to see the great variety of types that are to be found. *Dilepis* has a double crown of hooks as do *Monopylidium*, *Anomotaenia*, *Liga*, *Parvirostrum*, and five other genera. Nine genera are defined as having a single crown of hooks and seven are unarmed, while *Angularia* is stated to have "a zigzag crown of numerous hooks (about 50)" and *Dipylidium* several rings of rose thorn hooks. Almost every possible combination of pore arrangement with reference to the margin and of the genital ducts to the excretory ducts is found. In *Dilepis* the pores are unilateral and the ducts pass dorsal to the excretory vessels and nerve, in *Choanotaenia* the pores are irregularly alternate and the ducts pass between the excretory vessels and dorsal to the nerve, in *Liga* the pores are regularly alternate and the ducts pass dorsal to the excretory vessels and nerve, in *Cyclorchida* the pores are unilateral and the ducts pass between the excretory vessels, *Diplidium* has a pore on each side and a double set of reproductive organs, and in *Anonchotaenia* the pores are irregularly or regularly alternate and the ducts pass ventral to the excretory vessels and nerve. The number of testes varies from one to 50 in the different genera. The shape of the hooks differentiates the family from the *Davaineidae* as defined by Ransom, but on the other hand some species of *Hymenolepis* have hooks much like those of the *Taeniidae*, and moreover, according to Ransom's statement, they may be anything but hammer-shaped. The character of the uterus is not diagnostic since the genus *Catenotaenia* is described as having a uterus consisting of a median stem and lateral branches which is like that in *Taeniidae*.

Fuhrmann (1907) gives a classification from which two or three quotations are now made:

"IV Familie *Davaineidae*

"Scolex mit einfach gebautem Rostellum, das mit einem doppelten Kranz sehr zahlreicher, meist sehr kleiner hammerförmiger Haken bewaffnet ist. Genitalorgane einfach oder doppelt, Genitalpori beiderseitig, einseitig oder unregelmässig abwechselnd.

"V *Dilepinidae*

"Scolex mit oder selten ohne bewaffnetes Rostellum, Saugnäpfe unbewaffnet. Genitalpori beiderseitig, einseitig, regelmässig abwechselnd. Genitalorgane selten verdoppelt, meist einfach.

"VI *Hymenolepinidae*

"Scolex meist bewaffnet mit einem einfachen Kranz von Haken, selten ohne oder mit nur rudimentärem Rostellum. Gleider immer breiter als lang, Genitalporen münden einseitig; die Geschlechtsgänge gehen über die beiden Langsstämme des Wasserfässsystem und den Längsnerven

durch. Die Hoden in der Zahl von 1 - 4. Vas deferens immer kurz, mit Samenblase, Uterus sackförmig, Eier mit drei Hüllen. In Säugetieren und Vögeln.

Fuhrmann (1908) places in the family Hymenolepididae the genera *Oligorchis*, *Hymenolepis* (recognizing the subgenus *Echinocotyle*), *Diorchis* and *Aploparaksis*. It is to be noted that the family Hymenolepididae is the most sharply defined of the three referred to above which include those genera which have been grouped more or less together by Ransom and by Braun (1894-1900). The family Davaineidae is fairly well defined by the character of the hooks and their arrangement, while the family Dilepididae contains a large group of genera differing rather widely in some respects, the most outstanding difference being in the character of the reproductive organs which may be either double or single in a proligotid. Braun (1894-1900) gives a classification which is upon less natural lines as is evidenced when the following points are mentioned: *Hymenolepis*, (recognizing the subgenus *Drepanidotaenia*) *Choanotaenia*, and *Dipylidium* are placed in the subfamily *Dipylidiinae* with a number of others, and *Davainea*, *Echinocotyle* and *Fimbriaria* in the subfamily *Davainiinae*.

The genera which were placed in the family Hymenolepididae by Fuhrmann (1907) are *Oligorchis* Fuhrmann (1906a) *Hymenolepis* Weinland 1858, *Diorchis* Clerc 1903, and *Aploparaksis* Clerc 1803. A discussion of the historical data relating to these genera is given in the following pages.



## HISTORICAL ACCOUNT OF THE GENERA

## GENUS OLIGORCHIS FUHRMANN 1906

Fuhrmann (1906a: 217) describes the type species of this genus under the name of *O. strangulatus*. The material was taken from *Elanoides purcatus* (L.) and was collected in Brazil. It is well described, and, since a discussion of its structure and a diagnosis of the genus is given in the systematic portion of this report, any further details seem unnecessary at this point.

## GENUS HYMENOLEPIS WEINLAND 1858

This is the oldest genus belonging to the family and has had about fifteen times as many species assigned to it as to Haploparaksis Clerc 1903, which is the next largest in size. Since an extended study of the species assigned to it has been made, it is proper to trace rather fully its history, especially the points which are concerned in the present study.

The genus was first described by Weinland in 1858 as a result of his study of a number of pieces of a small tapeworm received from the collection of the Medical Improvement Society of Boston. The specimens were from an infant 19 months old, and had been obtained in 1842. Since the publication is rather inaccessible and since some very important characteristics are pointed out, it seems advisable to refer to the details which Weinland mentions at some length at this point. It was preserved in the collection of the society under the name of "*Bothriocephalus latus*," probably owing to the regularity and shortness of the joints. "Moreover, there is a yellowish spot, clearly visible to the naked eye, situated about the middle of each joint, which reminds us very much of the color and situation of the genital organs as known in *Bothriocephalus*," according to the account of Weinland.

"A careful examination, however, has taught us that there were in that phial parts of at least six different specimens of a very characteristic tapeworm, belonging neither to the genus *Bothriocephalus* nor to the genuine *Taeniae*,—which latter, when limited in our sense, comprehend, besides *Taenia solium*, only tapeworms of carnivorous mammals,—but to a group of *Taenoids*, whose members thus far had only been found in small omnivorous or insectivorous *Mammalia* (mice, shrew-mice, etc.) and birds. It is widely different from *Taenia solium*, and its true congeners, in the structure of its eggs, the situation of its genital openings, etc."

After a somewhat extended description of the external characters such as measurements, shape of proglottids, Weinland discusses the reproductive

organs as follows: "In relation to the genital organs, we have mentioned above the yellowish spots lying near the middle line in the anterior part of each joint, and it is for this that we have called the species *flavopunctata*. These spots are the testicles, appearing under the microscope as a globular gland, with another small one attached to it; this latter one runs out, toward the side of the joint into a long slender canal, in which lies the penis. The genital openings are situated all on one and the same side of the worm, while in all true taenias known thus far, they are found irregularly, now on one, now on the other side. The configuration of the uterus, also, differs greatly from that in the genuine *Taenias*. There is no main-stem in the midst with lateral branches, as in the latter; but, on the contrary, the eggs are crowded over the whole joint. It sometimes appears as if they were arranged in straight lines along the joint; but this is certainly owing only to the regular lines of muscular contractions. Only fresh specimens can decide ultimately the structure of the uterus. From a careful dissection of the younger joints, we should judge that it consists of globular blind sacs, located here and there in the joint, and connected by fine tubes terminating finally in the vagina. The most characteristic feature of this worm is its eggs, the number of which may be counted by thousands in each ripe joint. They are very large, measuring .054 millim. in diameter, and under a low power of the microscope appear as transparent balls with a yellow dot in them. With a higher power, we easily distinguish three distinct eggshells (Fig. 9, 1, a, b, c). The outside shell is translucent, elastic, cracking in sharp angles under pressure and only .0007 millim. thick; this shell is folded by application of glycerine. The second shell is membranaceous and irregularly wrinkled, thinner than the first, and immediately attached to it. . . . The large cavity which is formed by these two outside shells contains a fluid, in which swims the small globular embryo (measuring only 0.024 millim.), enclosed in a third shell, closely attached to it, but of considerable thickness (0.001 millim.). We cannot state with certainty that there are three pairs of spines to this embryo; if there are any, they must be very small."

It is interesting to note that Weinland points out as characteristics of the genus some which seem to be of almost universal occurrence in the species assigned to it at the present time, namely, three egg shells, unilateral genital pores, and a transverse sacular uterus. In all the descriptions of the species the only suggestion that there are but two shells is by Ransom (1909), in his account of *H. cantaniana* which reads as follows: "When they first enter the uterus, the eggs have but a single thin membrane and measure but  $20\mu$  in diameter. Later other membranes are developed, and the egg (Fig. 29) in the final stage of development possesses two well-defined shells, an inner one 27 to  $35\mu$  in diameter and an outer one 45 to  $60\mu$  in diameter. Between the outer and inner shell is an intermediate

finely granular layer limited by a very thin membrane internally and externally." That this "very thin membrane" is the third shell or the rudiment of it seems not at all improbable.

Concerning unilateral genital pores, the following species may be referred to. *Weinlandia asymetrica* Fuhrmann 1918 is described as follows: "nous avons observé que les pores sexuels qui sont unilatéraux peuvent se trouver, de temps en temps, mais très rarement, sur le côté opposé." Another observation is noted in *Weinlandia lateralis* in this report. Such irregularities may be referred back to the ancestral condition of this very large group of cestodes in which the position of the pores was probably irregularly alternate. Concerning the structure of the uterus, the only exception to the transverse sacular type that has been found is that of *H. pauciovata* Fuhrmann 1906, in which it is spherical in shape and centrally located in the proglottid.

Weinland gives a proposed revision of the taenoid cestodes in a footnote beginning on page 50, which is based primarily on the eggshell. It is briefly outlined as follows:

Family Taenioidea; 4 suckers on the head and with marginal genital openings.

Subfamily Sclerolepidota "with a hard, brittle, rather thick, and dark colored eggshell."

Genus 1. *Taenia*, uterus with median stem with lateral branches, head with two rows of hooks of the type of *T. solium*.

Genus 2. *Acanthotrias* Weinl. 1858 with three rows of hooks, type *Cysticercus acanthotrias* which Weinland described on page 64 of the same paper.

Genus 3. *Taeniarhynchus*, Weinl. type *T. mediocanellata*, without rostellum.

Genus 4. *Echinococcifer* Weinl. here belongs, *T. echinococcus*.

Genus 5. *Diplocanthus* Weinl. with a crown of bifid hooklets.

Subfamily Malacolepidota (Soft shelled tapeworms, shell thin and transparent).

Genus 1. *Hymenolepis* Weinl. The name is derived from the Greek words meaning membrane and shell. "Rarely 2 rows of hooklets on the proboscis." Uterus consisting of ball-like blind sacs.

Subgenus *Lepidotrias* Weinl. with three eggshells, type *T. murina* Dujardin.

Subgenus *Dilepis* Weinl. with two eggshells. Type *T. angulata*.  
Genus 2. *Proteocephalus* Weinl. No proboscis nor hooklets, eggs with 2 shells, head very changeable in shape. Type *T. ambigua* Dujardin.

Genus 3. *Alyselminthus* Zeder, containing only *T. cucumerina* of the dog, small spines arranged in a series of rows.

Since a discussion of the synonymy of most of the above divisions is given by Stiles (1903), it does not seem advisable to go into the details here, but since this study is especially concerned with the genus *Hymenolepis*, and its particular type of structure in order to determine which of the proposed new genera shall retain this name, I must now go into this somewhat in detail.

Grassi (1888) points out the synonymy of *Taenia diminuta* Rudolphi 1819, *T. leptcephala* 1825, and *H. flavopunctata* Weinland 1858. R. Blanchard (1891) gives a description of the anatomy of *H. diminuta* based on the work of Grassi (1888) Zschokke (1885-88) and recognizes the genus *Hymenolepis* Weinland. The important characters which distinguish it are stated as follows:

"Corps petit, filiforme. Tête petite, pourvue d'un rostre rétractile, bien développé et armé d'une simple couronne de 24 à 30 petits crochets, ou rudimentaire et inerme. Cou long. Anneaux en dents de scie, beaucoup plus larges que longs, en nombre rarement inférieur à 150. Pores sexuels marginaux, percés sur le bord gauche des anneaux, la face ventrale de ceux-ci étant celle qu'occupe l'appareil génital femelle. Appareil mâle formé d'un très petit nombre de testicules, le plus souvent de trois, dont deux dans la moitié droite et un dans la moitié gauche de l'anneau. Anneau mûr transformé en un sac plein d'oeufs clairs, arrondis ou oblongs, et entourés de trois coques très écartées les unes des autres. La coque interne enserre l'oncosphère et n'a pas d'appareil pyriforme; elle présente parfois un mamelon à chaque pôle. La larve est un *Cryptocystis* ou un *Staphylocystis*. La migration s'accomplit soit entre deux organes d'un hôte unique, soit, le plus souvent, entre deux hôtes différents, l'hôte intermédiaire étant un Insecte ou un Myriapode."

Blanchard placed in this genus 14 species giving a short diagnosis of each. These species are the following:

First Group—Armed *Hymenolepis*

<i>H. murina</i> Dujardin 1845	<i>H. pistillum</i> Dujardin 1845
<i>H. nana</i> von Siebold 1853	<i>H. tiara</i> Dujardin 1845
<i>H. microstoma</i> Dujardin 1845	<i>H. erinacei</i> Gmelin 1845
<i>H. furcata</i> Stieda 1862	<i>H. bacillaris</i> Goeze 1782
<i>H. uncinata</i> Stieda 1862	<i>H. acuta</i> Rudolphi 1819
<i>H. scalaris</i> Dujardin 1845	<i>H. decipiens</i> Diesing 1850

Second Group—Unarmed *Hymenolepis*

<i>H. relicta</i> Zschokke 1888	<i>H. diminuta</i> Rudolphi 1819
---------------------------------	----------------------------------

Thus the genus *Hymenolepis* was established. The genus grew by investigators referring previously described species to it, or by placing new ones in it until it has reached the present great size of about 200 species. The species found in birds have been brought together by the following investigators. Fuhrmann (1908) has the most extensive list thus far

published. It contains about 125 species listed under the host orders and again by hosts. Ransom (1909) catalogues the names of about 70 species with their hosts and references to the most satisfactory descriptions.

The literature dealing with this large collection of species is indeed anything but satisfactory since no extensive attempt has been made to assemble the important characters of the various groups of species and to determine what are the relative value of these characters. One may identify a cestode belonging to this genus only in one of the following ways. He may look up the descriptions of as many species as are available, compare the size, number and shape of hooks, arrangement of the testes, and other internal organs with those structures on his specimens or he may take one of the host lists, and look up the species described from the host from which his specimens were obtained. The process by either method is time-consuming and the result likely to be unsatisfactory because of the lack of sufficient details in many of the descriptions. The proposed grouping of the species incorporated in this report is a result of a comparative study of the descriptions of all the species and of the new species herein described from North American birds.

#### CHARACTERS PREVIOUSLY USED TO DIVIDE THE GENUS

The divisions of the genus *Hymenolepis* which have not yet been discussed have been made upon the character of the hooks. The division based upon the characters of the egg which was advocated by Weinland (1858) has been discussed above. Railliet (1892) proposed a grouping of the numerous species of cestodes of birds in particular into the two genera of *Drepanidotaenia* and *Dicranotaenia*. At the end of a note in this paper, which deals with some specimens of *Taenia tenuirostris* Rud., he defines these proposed new genera and remarks as follows:

"Puisque l'occasion se présente de parler des Ténias des Oiseaux, je tiens à signaler en passant la nécessité de poursuivre la division de ce groupe, entreprise déjà par R. Blanchard. Il est impossible, en effet, de laisser parmi les *Taenia* s. str., c'est-à-dire à côté des grands Ténias de l'Homme et des Mammifères, l'ensemble des Téniaïdés qui vivent dans l'intestin des Oiseaux.

"Aussi proposerai-je d'établir pour ceux-ci deux nouveaux genres, basés principalement sur la forme des crochets:

1. *Drepanidotaenia*, pour les Téniaïdés du type *Taenia lanceolata* Bloch, dont le rostre est armé d'une couronne simple de crochets uniformes, généralement en petit nombre, a manche beaucoup plus long que la garde, qui est toujours faible.

2. *Dicranotaenia*, pour ceux du type *Taenia coronula* Dujardin, qui ont une couronne simple de crochets uniformes, courts, généralement en petit nombre, à garde égalant ou surpassant également le manche en longueur, et formant avec la lame une sorte de petite fourche.

"Plusieurs autres divisions semblables devront être effectuées par la suite, mais j'ai visé principalement ici les Téniaés des Oiseaux domestiques, les seuls dont j'aie pu jusqu'à présent m'occuper d'une façon suivie."

Railliet gives no list and mentions no species other than those named as the types. Stiles (1896) recognizes the above genera and groups several species under each with diagnoses of each and a key. The difficulties which are encountered when an attempt is made to use the above characters as distinctive of genera are very evident in Stiles' classification. He includes in the genus *Dicranotaenia* *Amoebotaenia cuneata* Linstow 1872 (= *Dicranotaenia sphenoides*) which has 15 to 20 testes and alternating genital pores. Along with the above species he includes *H. coronula* Dujardin 1845, *H. aequabilis* Rud. 1809 and *H. furcigera* (Krabbe) 1869. In the genus *Drepanidotaenia*, Stiles places *Monopylidium infundibulum* (Bloch) 1779, which is like *Amoebotaenia cuneata* in that it has numerous testes. Here also are placed *H. tenuirostris* (Rud.) 1819, *H. setigera* (Frölich) 1789, *H. collaris* (Batsch) 1786, (= *H. sinuosa* Zeder 1800), *H. anatina* (Krabbe) 1869, *H. lanceolata* (Bloch) 1782, *H. fasciculata* Ransom 1909 (= *H. fasciata* Rud.) 1809, and *H. gracilis* (Zeder) 1803. It is seen by the classification outlined above that much difficulty is encountered in bringing such widely different forms into the same genera. An interesting note is found in the addendum, (p. 60) of Stiles (1896) as follows:

"Choanotaenia: Railliet proposes a new genus, with *Taenia infundibuliformis* Goeze as type in the following words: Le *Taenia infundibuliformis* Goeze, que j'avais placé provisoirement dans le genre *Drepanidotaenia*, s'en distingue par le grand nombre des testicules, et d'une manière générale par la constitution de l'appareil reproducteur (Crety). Il mérite donc de devenir le type d'un nouveau genre *Choanotaenia*. *Ch. infundibuliformis*, intestin de la poule."

"Although I recognize the great difference in organization between *T. infundibuliformis* (as described by Crety) and the other species of *Taenia* which have been placed in *Drepanidotaenia*, and am inclined to consider it generically distinct from these worms (see p. 45), and although I have the highest regard for the opinion of my colleague and for his keen foresight, particularly in systematic questions, I prefer to reserve judgment upon his new genus until its type species and a few allied forms are more thoroughly understood, especially as it appears to me that *T. infundibuliformis* as determined by various authors is rather a heterogeneous and collective species."

Thus it is apparent that uncertainty was at once present in the minds of the first workers in these new groupings as to the importance of the characters which they had assigned to them, when they made comparisons with the internal structures.

Cohn (1901) divided the genus *Hymenolepis* into the subgenera *Hymenolepis*, which contained those species with more than ten hooks or with

rostellum rudimentary and unarmed, and Drepanidotaenia, which included those with eight to ten hooks. Neither of the above subdivisions have come into general use due to the difficulty of accurately dividing a group of species on the basis of the number of hooks or their shape. The difficulty is very real when the shape is used since there are all grades of intermediate forms between the two extremes, and such a system would be mathematical, a very unsatisfactory method due to the differences in position in which different observers might select in which to view the hooks, and the errors of measurements of different investigators. It also happens in many cases that the scolex is not obtained or it may not be possible to count the hooks or to observe their shape accurately, due to the state of contraction of the rostellum. If, in such a case, the scolex is sectioned, there is always the possibility that hooks may be torn off by the knife or cut into pieces, leading to an unreliable count and view of the shape. It is not infrequent also that individual hooks are lost, and, if this happens, the fact is sometimes difficult to detect from the position of the remainder. A very striking illustration of the slight value which may be placed upon the characters of the hooks aside from the internal structures is found in *Weinlandia introversa* and *Weinlandia macrostrobilodes*. It is noted in the descriptions of these forms that the hooks are almost identical in shape, so similar in fact that one might easily interpret any discrepancies to inability to obtain a proper view; the hooks are also very near to each other in size (*W. macrostrobilodes* 15 to 16 $\mu$ , and *W. introversa* 17 to 20 $\mu$ ) and number.

Moreover, the arrangement and general structure of the internal organs are almost identical except for the differences in size recorded in detail in the description of *W. introversa*. There are two very outstanding differences, however, which separate these two species very widely from each other. These are the differences in the rostellum, which in *W. introversa* it is an introvert, and in *W. macrostrobilodes* is retracted as a solid muscular organ, and the difference in the size of the internal organs and of the strobila for the details of which the reader is referred to the descriptions of the species.

A little discussion of the manner of retraction of the rostellum seems proper at this point. It would appear that if the characteristic difference between the muscular arrangement of the rostellum which results in this organ being retracted as an introvert in the one case, and as a solid muscular organ in the other, had been observed by former investigators, they would have attached as much importance to it as they did to the number and shape of the hooks. The differences in the muscular arrangement are indeed marked as is apparent when figures 63 and 72 are compared. Yet this difference was not fully established until sections were studied; thereafter the arrangement could be made out in properly prepared toto mounts.

Another subdivision of the genus *Hymenolepis* remains to be discussed. Blanchard (1891) groups the cestodes with armed suckers into three genera, namely: *Echinocotyle* R. Blanchard 1891, *Davainea* R. Blanchard and Railliet 1891, and *Ophryocotyle* St. Friis 1870. The genus *Echinocotyle* was based upon the anatomy of *Echinocotyle rosseteri*, the internal anatomy of which is imperfectly known, but which had the suckers armed with three series of hooks. But one species was placed in this genus by R. Blanchard; later Fuhrmann (1908) included four others besides the type mentioned above and considered it as only a subgenus. The value of such an external character, however, seems to be of little importance.

In connection with the study of the scolex and other external features as systematic characters, it is interesting to note the conclusions arrived at by Fuhrmann (1918) as a result of his studies on the anatomy of *Fimbriaria intermedia* Fuhrmann 1914 and *F. fasciolaris* (Pallas 1781). The relative importance of the pseudoscolex as compared with the internal structures as a systematic character is very fully considered, and the conclusion is reached that it is of only secondary importance and that the genus should be placed in the family Hymenolepididae.

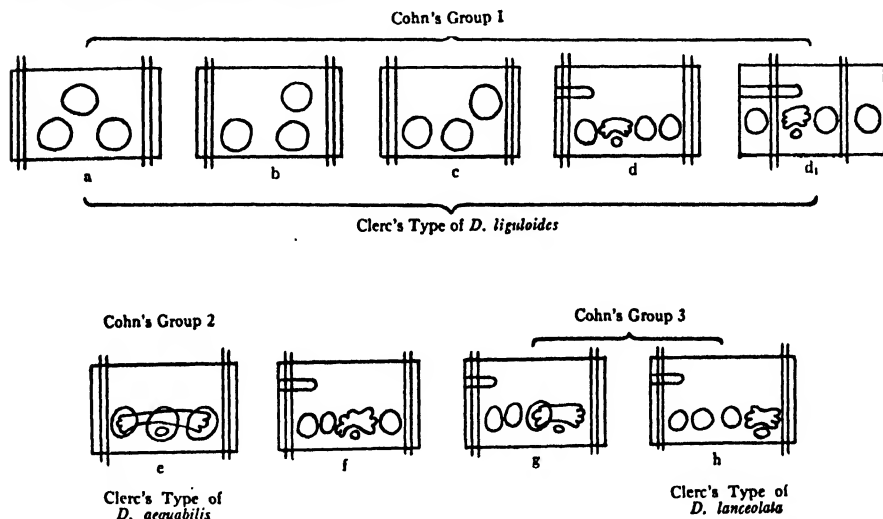
Concerning comparative studies upon the species assigned to the genus *Hymenolepis*, there seems to be few of any importance because of their limited range. Fuhrmann (1906d) compares the hooks as to number and shape in a considerable number of species. On page 625 he gives a diagram showing the relationships between the different shapes, and mentions a number of species in connection with each type. He also discusses in a general way the scolex, excretory system, musculature, and cirrus sac. Fuhrmann (1906e) compares the reproductive organs of a limited number of species by taking into account the relative position of the testes to each other and to the ovary. He defines nine groups which may be described as follows, using the letters designating his figures:

- a,—two testes posterior and one anterior and median to both posterior organs, typical species *H. megalorchis* Lühe 1898, *H. microps* (Dies.) 1850, *H. coronula* (Duj.) 1845, *H. filirostris* Wedl. 1856.
- b,—arrangement like above but anterior testis in front of antiporal posterior, no typical species named.
- c,—arrangement a, except anterior testis is lateral to antiporal posterior testis, typical species *H. farcimialis* (Batsch) 1786, *H. interrupta* (Rud.) 1809, *H. longirostris* (Rud.) 1809, *H. megalops* (Nitzsch) 1829, *H. gracilis* (Zeder) 1803.
- d,—two testes antiporal and one poral to the ovary, in a transverse row, typical species *H. bisaccata* Fuhrmann, *H. micrancristrola* (Wedl).
- d<sub>1</sub>,—testes like above but lateral ones outside excretory ducts, typical species, *H. multiformis*.
- e,—testes like d, but the middle one dorsal to the ovary, typical of *H. himantopodis* (Krabbe), *H. fragilis* (Krabbe), *H. villosa* (Bloch), *H. aequabilis* (Rud.), *H. tenuirostris* (Rud.), *H. breviannulata* Fuhrmann, and *H. microscolecina* Fuhrmann.
- f,—two testes poral to ovary and other antiporal, typical of *H. brachycephala*.



- g,—all three testes poral to ovary but antiporal one dorsal to ovary, typical of *H. setigera* (Fröhlich), *H. unilateralis* (Rud.) Fuhrmann, *H. elongata* Fuhrmann.  
 h,—all three testes entirely on the poral side of the ovary, typical species *H. lanceolata* (Goeze).

The difficulty in using the above groupings arises in placing the ovary correctly for there are all degrees of variation between some of them, as illustrations of which we may mention *H. pauciovata* Fuhrmann 1906, *H. serrata* Fuhrmann 1906, *H. bilateralis* v. Linstow 1905, and others in which the ovary extends beneath the testes, it often being necessary to use the shell gland or vitelline gland instead of the ovary as the point of decision. While there is some value to the above grouping there is less regularity and it is less clearly defined than when the relative position of the testes is used as a criterion.



TEXTFIGURE 1. DIAGRAM SHOWING THE RELATION BETWEEN THE GROUPINGS OF SPECIES OF HYMENOLEPIS MADE BY FUHRMANN, COHN AND CLERC

(The figures are after the patterns made by Fuhrmann)

Clerc (1903: 308) distinguishes three types of testicular arrangement, based partly upon other observers' work in the subgenus *Drepanidotaenia* which he designates as follows:

- a,—type of *D. liguloides*. "Le premier type a été déjà décrit par Cohn. Il est caractéristique pour les espèces à proglottis relativement long, ce qui permet à un des testicules de se loger en avant de l'autre."  
 b,—type of *D. lanceolata*, "établi par Wolffhügel et par Cohn, ne renferme que deux espèces, *D. lanceolata* et *setigera*, que j'ai décrites plus haut. Il est caractérisé avant tout par le fait que les glandes femelles sont très peu volumineuses et entièrement logées dans la moitié du proglottis opposée au pore génital. Les testicules sont, par contre, très volumineux et disposés suivant une ligne transversale."

c,—type *D. aequabilis*, "comme les deux types précédents, caractérisé par un très grand développement des testicules, mais il en diffère par la position et les dimensions des glandes femelles. Ces dernières sont médianes, rigoureusement ventrales et occupent souvent tout le champ ventral du proglottis, entre les vaisseaux excréteurs."

Cohn (1904) in a footnote (p. 244, 245) discusses the arrangement made by Clerc and described above, and defines these three groups as follows:

1. Hoden inkongruent, einer proximal, zwei distal. Weibliche Drüsen wenig in die Breite entwickelt, mehr-weniger median.
2. Alle drei Hoden auf einer Seite, während die weiblichen Drüsen auf der anderen Seite liegen.
3. Hoden kongruent, einer median. Weibliche Drüsen stark in die Breite entwickelt.

This, it is seen, is but little different from that outlined by Clerc except that the ovary enters into all three, while Clerc leaves it out of account in the *D. liguloides* type. The diagram in textfigure 1 indicates the relationships between these three suggested groupings.

#### GENUS DIORCHIS CLERC 1903

This genus is relatively young and consequently one finds few historical data. It was established by Clerc (1903: 281) with *D. acuminata* as the type. He defined its characters as follows:

"Cestodes d'oiseaux à proglottis très nombreux et courts. Crochets du rostellum en petit nombre et en couronne simple.

"Pores génitaux unilatéraux. Deux testicules par proglottis. Muscles longitudinaux divisés en deux couches, dont l'interne ne comprend que huit faisceaux.

"L'utérus sacculaire remplit tout le proglottis mûr."

Fuhrmann (1906e: 738) places the genus *Diorchis* in its present group of genera saying as follows:

"Das Genus *Hymenolepis* bildet mit den Genera *Aploparaxis* Clerc, *Diorchis* Clerc und *Oligorchis* Fuhrmann eine sehr natürliche Gruppe, welche manchen gemeinsamen Zug in der Art der Bewaffnung und der Anatomie zeigt und deshalb sehr wohl eine besondere Unterfamilie der Cyclophylliden zu bilden berechtigt ist."

In the next paragraph Fuhrmann gives a diagnosis and names the subfamily *Hymenolepinae*. In 1908 he places these four genera in the *Hymenolepididae*. Ransom (1909) places these four genera in the subfamily *Hymenolepidinae* giving a diagnosis and list of species with references to their descriptions.

#### GENUS HAPLOPARAXIS (CLERC) 1903

The genus was first set up by Clerc (1902a) under the name of *Monorchis* to contain those species of cestodes which possessed but one testis in a proglottid. In 1903 he displaced the name *Monorchis* with *Aploparaxis*\*

\* The name should be spelled *Haploparaxis*.

since he had found that the former had already been given to two species of trematodes. In the preliminary report Clerc includes six species as follows: *H. filum*, as type, *H. crassirostris*, *H. hirsuta*, *H. cirrosa*, *H. dujardini*, and a variety of *H. filum*, viz: *pseudofilum*, which he described as a new species. In the complete report of 1903, Clerc describes an additional new species *H. penetrans*, and reduces his former new species, *pseudofilum*, to a variety of *H. filum*. The complete list of species now placed in this genus appears in the systematic section of this paper, as well as a diagnosis of the genus.

## PROPOSED REVISION OF THE GENUS HYMENOLEPIS

As the information concerning the anatomy of the various species of *Hymenolepis* was brought together for comparison, it soon became apparent that the testes were usually the most satisfactorily described of the internal organs. Their position was usually stated, and, in a large percentage of cases, figured. This fact suggested the possibility of arranging a number of groups of species which might be made use of in constructing a key. As a further indication of the usefulness and the reliability of such groupings, it was noted, when a study of the material collected was undertaken, that the testes were invariably characterized by the same relative positions with reference to each other in all the proglottids of a strobila, and likewise, in other specimens of the same species. The few exceptions which may be found, and some are usually found, may be construed as abnormal or unusual, and as suggestive of the condition in the primitive ancestral forms of the group. This point is well illustrated by *Weinlandia lateralis* which has two testes placed on the posterior border and the third in front of and lateral to the antiporal posterior organ. The ovary is located behind and lateral to the anterior antiporal and lateral to the posterior antiporal testes, as is shown in figure 54. This position is characterized by its extreme regularity; not a single variation has been noticed. In the young proglottids where the early conditions are first visible, the testes are so placed, which indicates that these are the positions where the testes are fundamentally located, and that they are not pushed into it by the pressure of the very large cirrus sac and the ovary, even when these organs are fully developed.

Species with the testes in a transverse row are the most constant with respect to the position of the testes. As examples of this may be mentioned *Hymenolepis lobulata* and *Hymenolepis cuneata* which have two testes on the poral side of the ovary and vitelline gland and one on the antiporal. The most outstanding exception to this is *Hymenolepis sacciperum* in which the testes are arranged two antiporal and one poral in about 95 per cent of the proglottids, while in the remainder either the arrangement differs from this or the number is other than three. This case is discussed more in detail later and an explanation offered for each of these irregularities. In a general way it may be stated at this point that they are believed to indicate the ancestral condition of the group, and that the various types of testicular arrangement found in the present species have developed from a primitive form with no fixed arrangement. A further point of interest is that among the species which do not have the testes arranged

in the same manner in all the proglottids of the strobila, there are some which have a very variable pattern, as does *Wardium variabile*, while in *Weinlandia microcirrosa* the variability is restricted within certain limits. In the latter, two of the testes are always posterior and the third anterior to the antiporal testis, but may be either medial, lateral, or directly anterior to it. In this species the arrangement is considered to be sufficiently limited to be included in the genus *Weinlandia*, which is characterized by having two testes posterior and one anterior to the antiporal testes. In other words, from a phylogenetic standpoint, the species has become sufficiently stable in its arrangement to indicate to what group of species it is the most closely related.

In the study of the anatomy of the species collected from American birds, several morphological details have been found which indicate that the testes of the species of *Hymenolepis* are compound organs. A discussion of these data is given in the following pages and under the following headings: (1) the irregularity in the number and branching of the vasa efferentia, (2) the lobing of the testes, and (3) the number and irregularity in position of the testes in *Hymenolepis saccipherium*.

Early in the comparative study of the species, the arrangement of the vasa efferentia suggested a possible relationship between the testes. As an illustration, in *Hymenolepis cuneata* (Fig. 50) the ducts from the two poral testes join and then their common duct unites with the one from the antiporal testes to form the vas deferens. In a species which had two testes poral and one antiporal, if the ducts from the posterior organs joined first, it would indicate that the anterior testis was homologous with the antiporal testis in *Hymenolepis cuneata* and would belong to the same natural group. As a result of this, the different patterns of testes arrangements may be considered to have risen through a rearrangement of that pattern found in the primitive form. As an illustration, Ransom (1902) gives a figure of the arrangement in *Hymenolepis megalops* (Fig. 15) in which the two antiporal ducts joint before uniting with the poral duct. To correlate this with the arrangement found in *H. cuneata*, the two poral testes would have to be shifted to the antiporal position, a seemingly impossible rearrangement, and indicating that these two species would belong to different natural divisions. A very real difficulty was at once encountered in the literature since there are only about seven descriptions of species in which there is any reference to the manner of union of the vasa efferentia; most of these are noted only in figures, and no statistical records of any sort given as to their regularity. Upon these grounds, it would be impossible to secure enough data to make anything like a satisfactory arrangement of such an exceedingly large number of species in a key by means of which one would be able to classify a cestode of this genus which he might have.

The study of the vasa efferentia in the material available revealed some interesting facts concerning which a rather detailed discussion of

several species seems now advisable. In *Weinlandia microcirrosa* (Fig. 1) there were found in four consecutive proglottids, which were examined in frontal section, all of the possible patterns of union of the vasa efferentia. In figure 1a the ducts from the two posterior testes join first, in 1b and 1c, the ducts from the two antiporal join first, while in 1d all three join at the same point. In *Weinlandia macrostrobilodes* one of the seven proglottids of which the arrangements are represented in figure 2e, has the ducts from the three testes all joining at the same point, while in all the others figured those from the two antiporal testes join first.

In some proglottids, more than one duct from a testis has been observed. These may unite and their common duct join that from another testis, as they do in figure 1c, or they may remain separate as in figure 4c. If it be assumed that the testes of *Hymenolepis* have been reduced in number from, say six in the ancestral form to three in the present types by the uniting of testes, it seems possible that the ducts have also united or that some of the primitive ducts have persisted and others have not. It is possible upon this basis to explain the diversity of pattern in species which probably have a constant pattern. Take as an illustration the pattern shown in figure 4c; if ducts Nos. 1 and 2 should fuse, retaining the position of No. 1, or that 2 should fail to develop, it would give the pattern found in figure 4a, while if, on the other hand, No. 2 became the functional duct, the result would be the pattern shown in figures 1d and 2e. Some of the patterns show considerable evidence for the fusion of the ducts, as for example, figure 4b, where there are two ducts from the poral testis, with a cross connection between them. If in this instance the posterior antiporal testis is a compound structure made up of three simple organs, each originally with a single duct, and the present single duct from it made up of the three primitive ducts and the poral testis made up of two simple organs, one can readily determine the original pattern. Another interesting pattern in this connection is that shown in figure 3e, which indicates that the single duct from the anterior antiporal testis is made up of three ducts or that it contains two and the single duct from the antiporal posterior testis contains two, either of which would result in the pattern shown. Figure 3d is suggestive of the union of the ducts from two testes resulting in a different pattern. If these had remained separate as far up as is indicated, the result would be a pattern similar to that found in figure 2e, where all the ducts join at the same point, or if the vas deferens had remained simple as far up as the opening between its two portions, the arrangement would be like in figure 4a. An examination of the exceedingly complex patterns shown in figures 6, 10, and 11 reveals the fact that any pattern can be obtained by considering that the testes are compound and that their ducts are formed by the union of the primitive ducts or by the failure to retain some of the primitive ducts.

Reference has been made above to the probable number of testes which have entered into that organ in the present condition, namely that there is a possibility of three in the anterior antiporal testis in figure 3e, or two in both the antiporal testes on a basis of the arrangement of the ducts. Several proglottids have two distinct ducts to a testis, namely figures 2a, b, f, 4c, and several in the proglottids figured from *Weinlandia planestici*, as in figures 6, 10, and 11. Three instances are shown in figure 6 of a testis having three ducts, and one in figure 2c. The evidence for a larger number of testes entering into that organ of present forms rests on Fig. 2d, which shows four ducts attached to the anterior antiporal testis.

A further indication of the compound nature of the testes is to be found in their being lobed. These organs are found to be regularly lobed in *Weinlandia macrostrobilodes* and *Weinlandia introversa*. The most interesting species, however, in this connection is *Hymenolepis sacciperium*, which is further characterized by the unusual variability in the number of testes discussed at length in the next paragraph. It is not uncommon for the testes to be lobed or constricted anterioposteriorly as is shown in proglottids in figure 44. Those which have but two testes, one on each side of the ovary, as is found in Fig. 44h, can be explained by considering that the two testes on either side in proglottid e have united and the constriction indicates the plane of fusion. Proglottid i indicates that the two on the poral side only have joined and j suggests that the two adjacent to the ovary on the antiporal side have fused. An interesting fact in this connection is that no testis was observed which had a constriction that did not have it directed along the anterioposterior axis of the strobila. These testes were studied in sections and found to be single organs and not to be due to separate organs overlapping one another, which would give this effect in toto mounts. Unfortunately in this species, the vasa efferentia were so poorly defined and lay so close to the testes that they could not be traced with any degree of certainty beyond the region of the vas deferens. The arrangements of the ducts indicated in figure 5 have some interesting irregularities and are suggestive of fusion of the ducts and testes.

The number of testes found in the proglottid also is another indication that there is a change taking place in the number of testes in this group of cestodes. It is only occasional that one finds a number other than three, but one does find in almost any species proglottids with one, two, and four testes in a proglottid. One of the species studied, however, is interesting in this respect. A careful examination of almost 1400 proglottids in two specimens of *Hymenolepis sacciperium* showed that in one specimen 5 per cent and in the other 7 per cent of the total in each possessed a number other than three or an arrangement other than that typical for the species. A representative figure of each of these types of arrangements is shown in figure 44. Of the total number, 1307 had the typical arrangement shown

in i and j or two testes antiporal and one poral to the ovary. The numbers of each of the other types found are as follows: of the type shown in proglottid c 29, d 8, e 5, f 20, g 16, and b, only 2.

It is now necessary to discuss some of these conditions in order to see how they may have come about. The presence of one testis on each side of the ovary has been referred to above as being possible through a fusion of two testes in each of these respective positions. The relative size of the testes is often evident as where there is only one it is invariably much larger than either of those where there are two. The lobing or constrictions in these organs in the anterioposterior axis has been referred to above and is frequently evident. The arrangements where there are two on either side of the ovary or two on the poral side and one on the antiporal may be explained on the basis that either fusion has or has not taken place in that location. The fact that so many proglottids (20) were found which contain but two testes on the antiporal side is believed to be an indication that this species is still somewhat unstable and shows some relation to another group of species containing only two testes. This may have occurred by fusion or by a failure of the poral testis to develop. Indeed, one sometimes finds groups of cells in the position of the poral testis which stain weakly in a manner similar to those in the testes and these undoubtedly are reproductive cells.

The evidence presented above indicates that each of the three testes of the species assigned to the genus *Hymenolepis* has been formed phylogenetically by the fusion of at least four simple testes. This has been presented under the following headings: (1) number and irregularity in the arrangement of the vasa efferentia; (2) lobing of the testes, and (3) the irregularities in the number and arrangement of the testes in *Hymenolepis saccipherum*.

There is considerable basis for believing that the evidence presented above does not indicate a splitting in the testes rather than a union. In first place, the ducts are found to be irregular in the youngest proglottids in which they can be recognized indicating that the irregularities are present from the beginning of their development. There is no increasing complexity in the vasa efferentia in proglottids in an anterio-posterior series. Again, the testes, as compared with the ducts, may be said to be physiologically the most active, and if splitting were taking place the testes would be already divided or lobed, and the duct divided only nearest the testes. The contrary is found to be the case when the figures are examined, as for example in figure 2f the two ducts from the anterior testis approach very near to each other at the testis but are widely separated at their opposite ends. A similar arrangement is to be observed in figure 2a, b, d, and 3e. In the third place, more than one vas efferens may connect with a lobe of the testis and with no regularity of position on the



lobe. This is the condition to be expected since the lobing of the testes would probably disappear before the complete union of the ducts. In the fourth place, considered from a phylogenetic standpoint, the most highly developed group of cestodes might be expected to be found in the most highly developed hosts. The occurrence of the members of the Hymenolepididae in birds and mammals is in support of the conclusion that the testes are compound since the cestodes parasitic in lower animals have more numerous testes.

## PHYLOGENY OF SPECIES IN THE GENUS HYMENOLEPIS

It is believed that the compound nature of the testes discussed in the preceding section has a direct bearing upon the relationships of the various groups of species which are to be made in the following section. An attempt was made in the last section to show that the three testes found in the present species is the result of the fusion of several simple organs present in primitive forms.

Another characteristic, which has not been referred to as yet, and which is believed to be very important, is the position of the pore and the relation of the genital ducts to the longitudinal excretory canals. An outstanding fact is that the genital ducts are always dorsal to the longitudinal excretory canals in all the species studied and in all the proglottids. This fact is not so difficult to determine as it might appear for in many species it can be very readily ascertained from toto mounts by careful focusing with a high power lens. This depends, however, upon the nature of the cirrus sac and the excretory canal. If they are both small and lie close together, it is sometimes impossible to determine this point with certainty from a toto mount and sections then become necessary. This point has been carefully studied in all the species, and in several specimens of each where such a number was available, and not a single exception was found. In young proglottids the position of the earliest stage of the cirrus sac is dorsal to the excretory ducts. But three exceptions have been described which have come to the notice of the writer. *H. asymetrica* Fuhrmann 1918 has the genital ducts regularly passing above, but exceptionally they may pass between the excretory ducts. *H. spinosa* Linstow 1906 is described as having the genital ducts passing between the excretory ducts, and *H. clausa* Linstow 1906 has the cirrus sac above and the vagina ventral, the two merging and the pore being absent. A careful restudy of these species should be made with the view to determining the constancy and the importance of these facts. It may be that these are representative of distinct groups to which others of the incompletely studied species may belong.

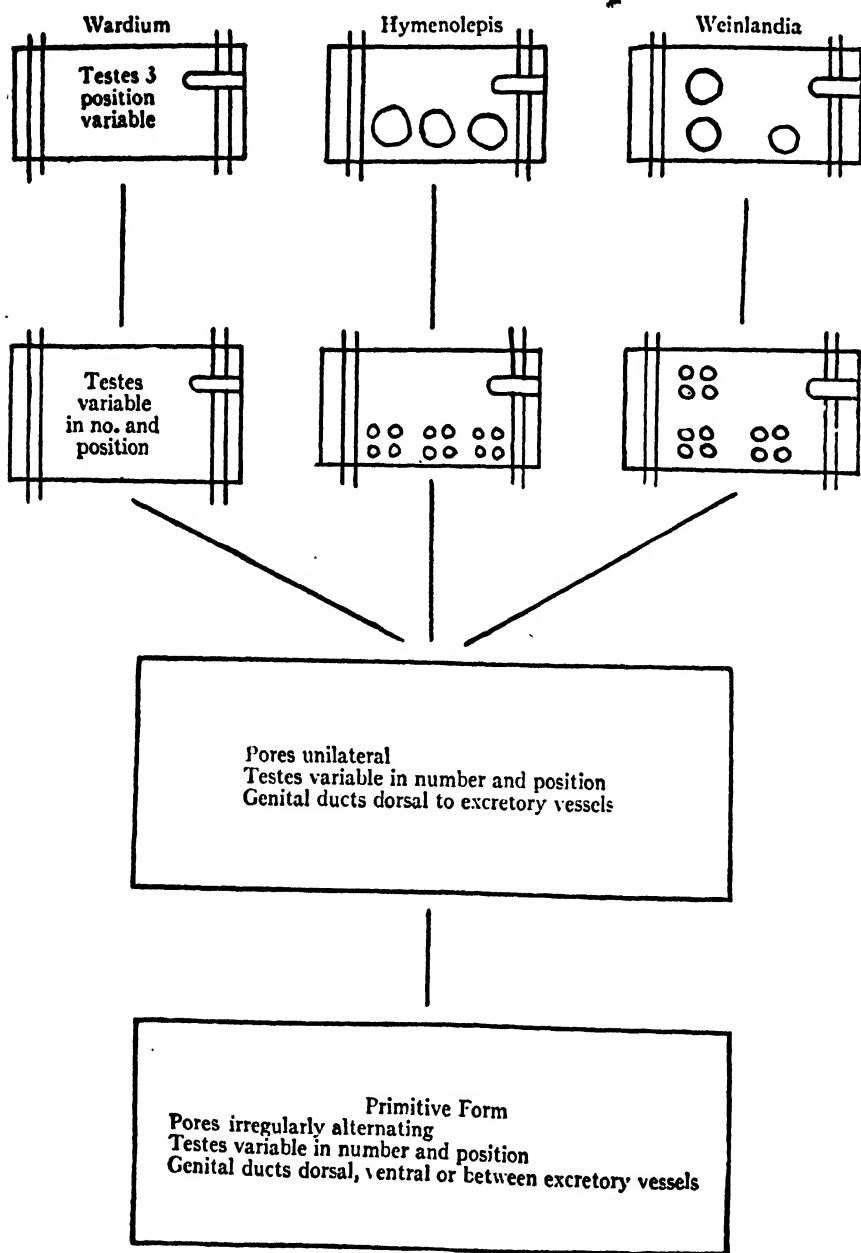
The regularity of the unilateral position of the genital pores has been referred to above, and the fact noted that but one exception has been observed, that of two proglottids in one specimen of *Weinlandia lateralis* having the pores on the opposite side from all the other proglottids in the specimen. It is believed that the regularity in position of the genital pores and genital ducts with reference to the excretory ducts is a very important morphological character which should be carefully determined in the future study of these forms.

It is now possible to formulate a conception of the ancestral form from which the various species assigned to the genus *Hymenolepis* have been derived. At least six testes and as many as twelve were present in a proglottid since the evidence presented above shows that at least two and possibly as many as four have joined to form a single testis of the present species. These testes had no definite pattern in the various proglottids of the strobila. The genital pores also alternated from side to side and the genital ducts were to be found dorsal, ventral or between the longitudinal excretory ducts. The first forms with fixed characters which diverged from this most probably had the genital ducts dorsal to the excretory canals and the pores unilateral. The most distinctive morphological character next to appear probably was in connection with the testes. It seems quite possible that the several testes first became localized in groups in definite locations in the proglottid. As an illustration, let us assume that there were twelve testes and that these became localized along the posterior border of the proglottid in groups of 4 or that two groups came to be found along the posterior border and the other in front of the posterior antiporal group. The next stage was seen in the union of these testes in those respective positions. In this manner it becomes apparent that the groups of species which have similar patterns of testes arrangement are fundamentally related, and that this relationship goes back to their common origin. They are thus separated from the species having other arrangements in a distinct and peculiar manner. The study of material and of descriptions reveals one group of species which have the testes arranged in an irregular manner. In the development of this group it may be assumed that the position of the groups of testes in the ancestral form did not become stabilized as to position in the proglottid, consequently when union took place, the compound organ retained this characteristic, and this group of present day species presents a variable pattern of testes arrangement.

Upon the basis of the above observations the author believes that the pattern of the testes arrangement is sufficiently reliable, easily enough ascertained, and goes back far enough in the phylogeny of the group to constitute a generic character. The position of the ovary in the proglottid and with reference to the testes at first seemed to be important, but it soon became apparent that this was much less clear cut and well defined since it usually overlaps the testes and sometimes it was necessary to use the position of the vitelline gland instead. This point is discussed more at length in the section on the history of the genus.

The following diagram (Textfig. 2) is believed to represent the relationships set forth above among the species which have been assigned to this genus.

**TEXTFIGURE 2. DIAGRAM SHOWING THE PHYLOGENETIC RELATIONSHIPS BETWEEN THE GENERA WARDIUM, HYMENOLEPIS, AND WEINLANDIA.**



## KEY TO SUBFAMILIES AND GENERA OF FAMILY HYMENOLEPIDIDAE

- 1(2) Four testes in each proglottid  
       Subfamily Oligorchinae Oligorchis
- 2(10) Three testes in each proglottid  
       Subfamily Hymenolepidinae.....3
- 3(7) Excretory vessels 4 in number, the genital ducts probably always passing dorsal to them. Scolex well developed. No pseudoscolex. Rostellum an introvert, not an introvert, or rudimentary, and armed with a single or double crown of hooks or unarmed.....4
- 4(5) Position of the testes variable Wardium
- 5(6) Testes in a transverse row Hymenolepis
- 6(7) Two testes posterior, the third anterior to the posterior antiporal testis  
       Weinlandia
- 7(3,8) Excretory vessels 4 in number. The genital ducts pass between the longitudinal excretory vessels. Longitudinal muscle bundles in two layers. Scolex well developed. Rostellum proboscis-like, with hooks distributed over its surface. Strobila well marked off into proglottids  
       Echinorhynchoetaenia
- 8(3,9) Excretory vessels 10 in number. Longitudinal muscle bundles in a single layer. Strobila well marked off into proglottids. Scolex well developed. Rostellum armed with a single crown of hooks Hymenofimbria
- 9(3,10) Longitudinal excretory vessels 3 to 11 in number. Scolex small. Pseudoscolex present. Strobila not marked off into distinct proglottids  
       Fimbriaria
- 10(11,1) Two testes in each proglottid  
       Subfamily Diorchinae Diorchis
- 11(1) One testes in each proglottid  
       Subfamily Haploparaxinae Haploparaxis

## FAMILY HYMENOLEPIDIDAE (ARIOLA) 1899

Family diagnosis: Cestodes with regularly from one to four testes in each proglottid. Rostellum either unarmed or armed with a single or double crown of hooks. Rarely the hooks are distributed over the surface of the rostellum. Genital pores unilateral. The uterus usually sac-like. Proglottids usually broader than long. Longitudinal muscle bundles in one or two layers.

Type genus: *Hymenolepis* Weinland 1858

The names of hosts of previously described species used in this paper are in agreement with the references cited, those of new species were obtained from the A. O. U. Check-list of 1910.

It should be indicated at this point that, due to the inadequate descriptions of many of the species, a number have been placed in the genera from the genus *Hymenolepis* with considerable doubt as to their relationship, and that before a final determination is made of any new material the original description should be consulted.

## SUBFAMILY OLIGORCHINAE

Subfamily diagnosis: *Hymenolepididae* having regularly four testes in each proglottid.

Type genus: *Oligorchis* Fuhrmann 1906

## GENUS OLIGORCHIS FUHRMANN 1906

Generic diagnosis: Four testes in a proglottid. A single set of reproductive organs in a proglottid. Genital pores unilateral, marginal or dorsal in position. Genital ducts pass dorsal to the longitudinal excretory vessels. Rostellum armed with a single crown of hooks.

Type species: *Oligorchis strangulatus* Fuhrmann 1906

## OLIGORCHIS STRANGULATUS FUHRMANN 1906

Fuhrmann 1906a: 217-218 (Fig. 26-29).

Host: *Elanoides furcatus* (L.).

Locality: Brazil.

Length 10 cm. Width 1 mm. Hooks 14 to 16,  $34\mu$  long. Ovary and vitellaria median, the former but slightly lobed. Testes irregular in position. Proglottids much wider than long.

## OLIGORCHIS DELACHAUXI FUHRMANN 1909

Fuhrmann 1909: 29 (Figs. 36-37).

Host: *Phalacrocorax africanus* (Gm.).

Locality: Egypt.

Scolex absent. Position of testes variable. Female sex glands not well developed, but are on the poral side of the proglottid. Cirrus sac reaches beyond the excretory vessels, its greatest diameter being at the poral end. Vagina is straight with seminal receptacle on its inner end. Proglottids appear from figure 36 to be much wider than long.

## OLIGORCHIS YORKEI (KOTLAN) 1923

Synonym: *Dilepis yorkei* Kotlan 1923.

Kotlan 1923: 59-63, (Figs. 1-4).

Host: *Megapodius brunneiventris* Mey.

Locality: Friedrich-Wilhelmshafen.

Length 15 to 20 mm. Mature proglottids 0.2 to 0.4 mm in width and 0.05 to 0.1 mm in length. Gravid proglottids are 0.3 to 0.5 mm in width. Rostellum armed with from 50 to 52 hooks in a double crown. The hooks of the anterior row are  $135\mu$  and those of the posterior row 148 to  $151\mu$  in length. Male and female reproductive organs median in position. Genital pores unilateral. Vagina short, narrow, and provided with a large receptaculum seminis. Ovary consists of 4 rounded or oval sacs, 1 in the poral half and 3 in the antiporal half of the proglottid, joined by thin walled canals which uniting form the oviduct. Uterus a thin walled sac, the wall of which atrophies in the posterior proglottids.

The internal structure of this cestode indicates its close relationship to those species already assigned to the genus *Oligorchis*. The double crown of hooks is not believed to be a character of sufficient importance to exclude it from the family Hymenolepididae. The constancy of the number of the testes in the numerous species of the several genera of the family is such an outstanding characteristic that it serves to separate this group of genera from other genera in a distinct and peculiar manner.

## OLIGORCHIS LONGIVAGINOSUS N. SP.

[Figs. 12-16]

The material which formed the basis of the following description was taken from the large intestine of *Pelecanus erythrorhynchos*, the white pelican in Yellowstone National Park, Wyoming, on August 10, 1917. Cotypes were deposited in the Ward collection, comprising five toto mounts and four sets of serial sections, catalogue numbers 25.22, and 25.23. For the most part the specimens are only fairly well fixed so that some of the details, such as vasa efferentia, could not be made out.

The specimens vary in length from 15 mm to 60 mm and in maximum width from 0.5 to 0.8 mm, according to the stage of sexual maturity and the condition of contraction of the worms when fixed. The width just behind the scolex is about 175-200 $\mu$ , while in the region where the male and female reproductive organs are well developed, it is about 500 $\mu$  and in the posterior portion where the uterus is fully distended, somewhat narrower, about 350 $\mu$ .

The scolex (Fig. 13) is a conspicuous portion of the worm, having a width up to almost 0.6 mm and a length of about 0.4 mm. The rostellum is strongly developed, being about 200 $\mu$  wide and about 100 $\mu$  long. The rostellum has, apparently, a single crown of large hooks the shape of which is indicated in figure 16. They are 88 to 92 $\mu$  long, and about 20 in number on one rostellum, which was retracted so that an accurate count could not be made. Another unretracted rostellum had 10 and another 12, both of which showed evidence of having lost hooks since those still remaining were twisted out of a regular arrangement, and on one side of one there were five set closely together, while on the other there was but one. An examination of the retracted rostellum appears to show a double crown of hooks, but when examined more closely, it seems quite evident that this is due to the position of the bases of the hooks when retracted. The blades of the hooks are directed outward showing that the rostellum is an introvert and the points of the hooks are observed to be in two rows. When the position of the dorsal root of the bases is examined, it is seen that those of the hooks of the posterior row are inside those of the anterior row which would result in the blade being carried farther outward than in the case of the anterior row. This difference in position of the points together with the fact that the scolex is tilted somewhat so that an exact lateral view is not obtained, would account for the appearance of two rows of hooks. An unretracted rostellum with a full complement of hooks would be conclusive proof of the exact arrangement but such is not at hand, and there is little probability of gaining more data by sectioning the one now under consideration. The general form, size, muscular arrangement, and structure of the proglottids agree with that of the other scolices and proglottids so that there is no doubt that they are all of the same species. There was no evidence of a double crown in any of the unretracted specimens, and, while the case is not clear, the probability is that there is but a single crown.

The testes are usually four in number but have no regularity of position. They are generally spherical in shape and dorsal in position in the center or posterior portion of the proglottid. Occasionally one is found beneath a lobe of the ovary. The position indicated in figure 15 is a little more common, but they may be in any position with reference to each other, dorso-ventrally as well as laterally. Figure 14 shows their location in three consecutive proglottids. The number of the testes varies slightly.



since in a count in 406 proglottids from 3 specimens, 99 were found to possess four testes, four had three, and one seemed to have five. The size varies considerably, occasionally one is observed one-half or two-thirds the size of the others in the proglottid. The cirrus sac reaches about half way across the proglottid, and gradually increases in size toward the inner end. It contains a small seminal vesicle and a large conspicuous cirrus. The latter extends the full length of the sac in a direct course, bends at the inner end and shortly connects with the internal seminal vesicle. The cirrus is large and conspicuous, being protruded in most of the proglottids of the strobila. Due to the poor fixation of the material, the vas deferens and vasa efferentia were not found, therefore no statement can be made concerning the existence of an external seminal vesicle.

The ovary (Fig. 15) is centrally located, usually a little anterior to the testes and ventral to them in position. It is usually divided into from four to six lobes which are rounded and knob-like at their distal end. The vitelline gland is a spherical or oval structure, dorsal to the central narrow portion of the ovary and without lobes. The vagina is unusually long, extending from the pore across the proglottid to the excretory ducts of the antiporal side and back again usually to the region of the pore, then across again to antiporal excretory duct and medially and posteriorly to the region of the ovary. The inner end enlarges to form a seminal receptacle which is conspicuous in the advanced stages of sexual maturity. The vagina opens into the shallow genital atrium ventral to the cirrus sac.

The position of the pore is not marginal but slightly dorsal on the left hand side of the proglottid, at about the junction of the anterior one-third and posterior two-thirds of the proglottid. It was noted that the pore seemed to change from side to side occasionally, but in no instance could this be positively determined since there were always at least two proglottids in which the pore or cirrus could not be located between the regions of change. In order to find out the exact structure at one of these points, one of these regions was sectioned. It was found that the muscles showed a twist of the whole chain and that the pores could be traced in a symmetrical row across the side of the strobila in the proglottids between those where it was on one side and those in which it was on the opposite side. This shows that there has been a twisting of the strobila in the process of fixation. The position of the ovary and testes ventrally and dorsally can be determined in toto mounts on the two sides of these regions and it is found that the pore is on the left hand side in each case.

The longitudinal muscles are poorly developed, and can scarcely be said to consist of two layers. Although the bundles are scattered dorso-ventrally, they are all about the same size. The longitudinal excretory vessels are four in number, and located near the lateral border of the proglottid. They are about the same size, and vary in position, being

pushed ventrally on the poral side by the cirrus sac, and turned somewhat laterally in places. The genital ducts always pass above the excretory vessels.

Of the species which have previously been described as having regularly four testes, *Oligorchis yorkei* (Kotlan) 1923, having two rows of hooks, approaches the nearest in general structure to the one described above. The most outstanding difference is in the nature of the ovary. In *O. yorkei* it consists of four separate sacs, one poral and two antiporal, connected by slender ducts uniting to form the oviduct, while in the above described form it consists of from four to six lobes with knob-like enlargements at the ends. The vagina is short in *O. yorkei* while in our species it is very long, and the cirrus sac is long and rather narrow and coiled, while in the latter it is short and bulb-like. The hooks also are different in that they are 50 to 52 in number in two rows and 135 to 151 $\mu$  in length, in contrast to about 20 in number and 88 to 92 $\mu$  in the above described form. The other three species described as having four testes are all so different in internal structure that it seems unnecessary to discuss them in detail. "

## DOUBTFUL SPECIES

### OLIGORCHIS PAUCITESTICULATUS FUHRMANN 1913

Fuhrmann 1913: 17 (Fig. 8).

This species has from 7 to 11 testes, but Fuhrmann placed it in the genus *Oligorchis* because of the presence of an external and internal seminal vesicle and revised his original description of the genus accordingly. However, the small and constant number of testes is such an outstanding characteristic of the numerous species of the family Hymenolepididae that it seems that this species should be excluded. The external and internal seminal vesicles, while they are very common and probably almost universal in the family, cannot be considered as anything else but a widened portion of the vas deferens, and are found in all degrees of relative size. They may serve as specific characters but seem scarcely of sufficient importance to cause the modification of generic and family diagnoses to admit species with other more evident unrelated characteristics.

### SUBFAMILY HYMENOLEPIDIDAE (FERRIER) 1897 RANSOM 1909 (EMENDED)

Subfamily diagnosis: Hymenolepididae with regularly three testes in each proglottid.

Type genus: *Hymenolepis* Weinland 1858.

## GENUS HYMENOLEPIS WEINLAND 1858

Three testes in a transverse row. Rostellum generally well developed and armed with a single crown of hooks, or it may be unarmed. Vas deferens with internal and external seminal vesicles. Genital ducts dorsal to the longitudinal excretory vessels, or exceptionally they may be between. Pores unilateral.

Type species: *Hymenolepis diminuta* (Rudolphi 1819) Blanchard 1891.

List of the Species in the Genus *Hymenolepis*

*All three testes lie close together or somewhat separated but not so placed that the ovary lies between any two of them. Ovary ventral, anterior, or posterior; but not lateral to the testes.*

1. *Hymenolepis breviannulata* Fuhrmann 1906.  
See Fuhrmann 1906c: 445 (Fig. 25).
2. *Hymenolepis longicirrosa* Fuhrmann 1906.  
See Fuhrmann 1906e: 751-752 (Figs. 17 and 18).
3. *Hymenolepis longivaginata* Fuhrmann 1906.  
See Fuhrmann 1906e: 752.
4. *Hymenolepis pauciovata* Fuhrmann 1906.  
See Fuhrmann 1906c: 447 (Figs. 28-31).
5. *Hymenolepis septaria* von Linstow 1906.  
See von Linstow 1906a: 177 (Fig. 21).
6. *Hymenolepis serrata* 1906.  
See Fuhrmann 1906c: 448 (Figs. 32-33).
7. *Hymenolepis solowiowi* Skrjabin 1914.  
See Skrjabin 1914: 467.
8. *Hymenolepis himantopodis* Krabbe 1869.  
See Krabbe 1869: 309; Fuhrmann 1906e: 748.
9. *Hymenolepis hemignathi* Shipley 1897.  
See Shipley 1897: 613-621, 10 fig.
10. *Hymenolepis spinosa* von Linstow 1906.  
See von Linstow 1906a: 178 (Figs. 24-25).
11. *Hymenolepis brasiliensis* Fuhrmann 1906.  
See Fuhrmann 1906c: 446 (Fig. 26).
12. *Hymenolepis furcifera* (Krabbe 1869).  
See Krabbe 1869: 306 (Figs. 176-178); von Linstow 1908: 38-39 (Figs. 1-2).  
See Krabbe 1869: 306 (Figs. 176-178) Linstow 1908: 38-39 (Figs. 1-2).

13. *Hymenolepis aequabilis* (Rudolphi 1810) Cohn 1901.  
See Krabbe 1869: 316-317 (Figs. 212-213 (*Taenia aequabilis*); Stiles 1896: 33-34 (Figs. 29-30) (*Dicranotaenia aequabilis*); Clerc 1903: 290-293 (Figs. 2, 16 & 24) (*Drepanidotaenia aequabilis*).
14. *Hymenolepis musculosa* Clerc 1903.  
See Clerc 1903: 303-3-5 (Figs. 17, 23, 29).
15. *Hymenolepis upsilon* Rosseter 1911.  
See Rosseter 1911: 147-160 (Figs. 1-9); Fuhrmann; 1913: 26 (Figs. 18-20).
16. *Hymenolepis villosa* (Bloch 1782) Wolffhügel 1899.  
See Krabbe 1869: 303-304 (Figs. 168-169) (*Taenia villosa*); 1882: 354-355 (Fig. 19-22). Wolffhügel 1900: 184-188, fig. 11.
17. *Hymenolepis compressa* (Linton 1892) Fuhrmann 1906.  
See Linton 1892: 108-110 (Figs. 83-92) (*Taenia compressa*). Kowalewski 1907: 775 (Figs. 7-11) 1908: 638-641 (Figs. 7-11).
18. *Hymenolepis baschkiriensis* Clerc 1903.  
See Clerc 1903: 288-290.
19. *Hymenolepis exigua* Yoshida 1910.  
See Yoshida 1910: 235 (Figs. 1-10).
20. *Hymenolepis fragilis* (Krabbe 1869) Fuhrmann 1906.  
See Krabbe 1869: 300-301 (Figs. 158-160) (*Taenia fragilis*). Fuhrmann 1906e: 747-748 (Figs. 11-12).
21. *Hymenolepis macrocephala* Fuhrmann 1913.  
See Fuhrmann 1913: 19-21 (Figs. 9-11).
22. *Hymenolepis nitida* (Krabbe 1869) Clerc 1902.  
See Krabbe 1869: 294 (Figs. 133-135) (*Taenia nitida*). Clerc 1903: 310-315 (Figs. 26, 27, 30, 31, 36, 38, 40-42).
23. *Hymenolepis nitidulans* (Krabbe 1882) Fuhrmann 1906.  
See Krabbe 1882: 353 (Figs. 16, 17) (*Taenia nitidulans*); Rosseter 1907: 36-39 (Figs. 1-15).
24. *Hymenolepis pachycephala* (von Linstow 1872) Fuhrmann 1906.  
See von Linstow 1872: 55 (Fig. 2-4) (*Taenia pachycephala*); 1904: 305. (Fig. 17-20) (*Drepanidotaenia pachycephala*).
25. *Hymenolepis rectacantha* Fuhrmann 1906.  
See Fuhrmann 1906c: 446-447 (Fig. 27).
26. *Hymenolepis trifolium* von Linstow 1905.  
See von Linstow 1905: 361-362 (Fig. 6-7).
27. *Hymenolepis lobulata* n. sp.  
See this, p. 43.
28. *Hymenolepis cuneata* n. sp.  
See this, p. 45.

*The two antiporal testes separated from the poral and the space thus formed occupied by the female reproductive glands.*

29. *Hymenolepis anatina* (Krabbe 1869) Cohn 1901.  
See Krabbe 1869: 287-288 (Figs. 114-116) (*Taenia anatina*). Schmidt 1894: 65-112 (Pl. 6) (*Taenia anatina*). Stiles 1896: 39-40 (Figs. 100-115) (*Drepanidotaenia anatina*).
30. *Hymenolepis bisaccata* Fuhrmann 1906.  
See Fuhrmann 1906c: 444-445 (Figs. 21-24).
31. *Hymenolepis capillaris* (Rudolphi 1810) Fuhrmann 1906.  
See Krabbe 1869: 307, (Fig. 179) (*Taenia capillaris*). This species is placed in this genus on the basis of the statement of the similarity between *H. capillaris* and *H. multistriata* made by Fuhrmann, 1908: 75, but its relationships are incompletely understood.
32. *Hymenolepis clandestina* (Krabbe 1869) Cohn 1904.  
See Krabbe 1869: 316 (Fig. 208-209) (*Taenia clandestina*). Cohn 1904: 243-246 (Figs. 9-12).
33. *Hymenolepis creplini* (Krabbe 1869).  
See Krabbe 1869: 317 (Figs. 214-215) (*Taenia creplini*). Cohn 1901: 304-307 (Figs. 31-33).
34. *Hymenolepis echinocotyle* Fuhrmann 1907.  
See Fuhrmann 1907: 532-533 (Figs. 37-38),  
The Zoologisches Museum der Universität, Berlin, very kindly gave material of this species to the Ward Helminthological Collection at the University of Illinois, Urbana; this was of great value in the author's work. This courtesy was greatly appreciated.
35. *Hymenolepis inermis* Yoshida 1910.  
See Yoshida 1910: 239-241 (Figs. 11-16).
36. *Hymenolepis kowalewski* Baczynska 1914.  
See Baczynska 1914: 219-221 (Figs. 51-54).
37. *Hymenolepis linea* (Goeze 1782) Wolffhügel 1899.  
See Krabbe 1869: 327-328 (Figs. 248, 249) (*Taenia linea*). Wolffhügel 1900: 189-190 (Fig. 112).
38. *Hymenolepis multistriata* (Rudolphi 1805).  
See Cohn 1901: 302-304 (Fig. 30).
39. *Hymenolepis retracta* von Linstow 1905.  
See von Linstow 1905b: 4 (Fig. 15).
40. *Hymenolepis meglahystera* von Linstow 1905.  
See von Linstow 1905b: 5 (Figs. 16-18).
41. *Hymenolepis orthacantha* Fuhrmann 1906.  
See Fuhrmann 1906e: 754 (Figs. 23-25).  
For this species also the author is indebted to the Zoologisches Museum der Universität, Berlin, which donated alcoholic material upon the request of Professor Ward to the Helminthological Collection at the University of Illinois, Urbana.
42. *Hymenolepis sacciperium* n. sp.  
See this report, p. 48.

*The two testes on the side toward the pore separated from the third, the space between occupied by the female reproductive glands.*

43. *Hymenolepis multiglandularis* Baczynska 1914.  
See Baczynska 1914: 211-214 (Figs. 40-44).
44. *Hymenolepis brachycephala* (Creplin 1829).  
See Krabbe 1869: 294-295 (Figs. 136-140) (*Taenia brachycephala*).  
Cohn 1901: 280-284 (Figs. 13-14).

*Ovary antiporal to the three testes but extending beneath the antiporal testis.*

45. *Hymenolepis przewalskii* Skrjabin 1914.  
See Skrjabin 1914: 471.
46. *Hymenolepis venusta* Rosseter 1896.  
See Rosseter 1898: 10-23 (Figs. 1-17).
47. *Hymenolepis ardeae* (Rudolphi 1819).  
See Fuhrmann 1906c: 451-452 (Figs. 37-39) (*H. ardeae*); 1906e: 740.  
Grateful acknowledgement is here made to the Zoologisches Museum der Universität, Berlin, for loan of material of this species for study.
48. *Hymenolepis elongata* Fuhrmann 1906.  
See Fuhrmann 1906e: 450 (Fig. 36).
49. *Hymenolepis setigera* (Frölich 1789) Cohn 1901.  
See Stiles 1896: 41-42 (Figs. 147-150) (*Drepanidotaenia setigera*);  
Clerc 1903: 298-302 (Figs. 3, 6, 7, 12, 22) (*Drepanidotaenia setigera*);  
Fuhrmann 1906e: 734.
50. *Hymenolepis bilateralis* von Linstow 1905.  
See von Linstow 1905b: 5-6 (Figs. 19-21).

*Ovary entirely antiporal to the three testes.*

51. *Hymenolepis lanceolata* (Bloch 1782) Weinland 1858.  
See Stiles 1896: 36-37 (Figs. 43-53, 54-55) (*Drepanidotaenia lanceolata*);  
Clerc 1903: 302-303, figure 4 (*D. lanceolata*). Ransom 1904: 14, 101-110 (Figs. 108-130).
52. *Hymenolepis tenuirostris* (Rudolphi 1819) Cohn 1901.  
See Stiles 1896: 43 (Figs. 165-172) (*Drepanidotaenia tenuirostris*);  
Cohn 1901: 326-327.

*Ovary on the poral side of the proglottid; all three testes antiporal to the ovary.*

53. *Hymenolepis biaculeata* Fuhrmann 1910.  
See Fuhrmann 1910: 21-22 (Figs. 17-21); 1909: 41.

*The two lateral testes placed lateral to the longitudinal excretory vessels on each side.*

54. *Hymenolepis microcephala* (Rudolphi 1819).Synonyms *H. leptoptile* Linstow 1901.*H. multiformis* Creplin 1828.

This is a very interesting species and deserves some discussion at this point. It has been recorded from *Ciconia ciconia*, *Pyrtherodias purpurea*, *Abdimia abdimia*, *Plegadis falcinellus*, *Ardea cinerea*, *Nycticorax nycticorax*, all of which are Ciconiiformes and from Europe and Africa. The species is described as having a length of from 100 to 300 mm. That this is a very characteristic form is indicated by the position of the testes. They are so placed that the two lateral ones are outside the excretory vessels, and, according to Cohn (1909: Taf. XI, fig. 14) in a transverse row, while Fuhrmann (1909) figures (Fig. 41, p. 43) and described them quite differently. Concerning the position of the genital pore, Cohn says: "Der Genitalporus liegt in der Mitte des Gliedrandes auf der rechten Seite auf einer konischen kleinen Erhöhung des Gliedrandes." Fuhrmann (1909) described the testes as follows: "Die Hoden zeigen eine sehr typische Disposition in dem sie was bei keiner anderen Hymenolepisart der Fall (mit Ausnahme von *H. multiformis* (Crepl.) so angeordnet sind, dass die beiden seitlichen Hoden ausserhalb der beiden weit nach innen verschobenen dorsalen ventralen Wassergefässpaare liegen. Der mediane Hoden liegt vor den weiblichen Genitalien."

The differences between the forms described by Cohn and Fuhrmann indicate that a re-examination of the specimens should be made, but the position of the testes with reference to the excretory vessels is so characteristic and stands in such marked contrast to the other species of the *Hymenolepis* group that a more careful study may result in the placing of this species in a separate genus. However, it is not possible to define exactly the characters of such a genus at present.

*Position of testes with reference to the ovary uncertain*

55. *Hymenolepis kempfi* (Southwell) 1921.Synonym *Dilepis kempfi* Southwell 1921.Host: *Phalacrocorax pygmaeus*.

Locality: North Lohtak Lake, Manipur, Assam.

Length 5 cm. Greatest width 1 mm. Posterior proglottids 900 $\mu$  broad by 400 $\mu$  long. Genital pores unilateral. Scolex 220 $\mu$  long by 400 $\mu$  broad. Rostellum about 170 $\mu$  long by about 160 $\mu$  broad. Hooks 20 in two rows, those in the posterior row 135 $\mu$  and those in the anterior about 175 $\mu$  in length. Testes in the median field and, according to figure 2, in a transverse row. Genital ducts pass dorsal to the excretory ducts. Uterus large and sac-like, with numerous out-pocketings, and reaching the excretory vessels on either side.

The small and almost constant number of the testes is such an outstanding characteristic of the genera and species of the family Hymenolepididae that it separates them from other Cestoda in a natural and distinct manner. After a study of this large number of species and of the data presented in this report, I do not believe this species ought to be excluded from the family on the basis of the double crown of hooks.

## DESCRIPTION OF NEW SPECIES

### HYMENOLEPIS LOBULATA N. SP.

[Figs. 32-39]

The specimens upon which the following description is based were collected by N. C. Gilbert at Bass Lake, Michigan, June 9, 1907, and are preserved in the collection of Professor H. B. Ward (No. 17, 180). In this study cotypes were selected comprising sixteen toto mounts and seven sets of serial sections, catalogue numbers 25.5 to 25.13 inclusive. They remain in the Ward Helminthological Collection at the University of Illinois, Urbana. The host was a single specimen of *Podilymbus podiceps* (Linnaeus) or the pied-billed grebe, and the organ the intestine.

*External anatomy:* The specimens vary from about 60 mm to 85 mm in length and from 2 to 2.5 mm in width. The width immediately behind the scolex varies from less than 100 to 225 $\mu$  depending upon the state of contraction of the strobila. The width at a number of points was measured in one specimen and is as follows: 20 mm from the scolex, 0.6 mm; 30 mm, 1.3 mm; 26 mm, 1.7 mm; 38 mm, 2mm; 68 mm, 2 mm; 86 mm, 1.5 mm. The proglottids are all much wider than long.

The scolex is 0.6 mm in diameter and almost spherical. The four rounded suckers are 0.25 mm in diameter and but slightly raised above the surface. The rostellum (Fig. 37) has a very interesting shape. It is long and slender, and generally twisted and coiled in preserved specimens. It is crowned at the tip by a knob-like enlargement which has deep marginal lobes, each of which carries a hook on its lateral margin. Anteriorly, this enlargement is but slightly arched. This enlargement is 0.1 mm in diameter, while the stalk part is but 35 $\mu$  in diameter by about 0.2 mm long. When the rostellum is retracted, the points of the hooks are directed anteriorly, while in the extended condition they are directed backward, showing that the rostellum is an introvert. In the partially retracted condition, they are placed regularly in two rows in a manner indicated in figure 34, while in the completely retracted condition they are closely packed together. The hooks are eight to eleven in number, 14 to 17 $\mu$  in length, and are shaped like figure 35. Of the scoleces examined, one had eight hooks, three had nine hooks, three had ten, one had eleven, and one had lost all but one hook.



The three testes are placed in a transverse row, two of them being on the poral side of the proglottid. The well-differentiated beginnings of the ovary and vitellaria are distinguishable in the space between and just posterior to the two poral and the antiporal testes in proglottids about 35 mm from the scolex. In this region the testes are oval in outline and 0.2 to 0.25 by 0.15 mm in size. The cirrus sac reaches to or slightly beyond the inner large ventral excretory vessel, and is surrounded by a layer, several cells in thickness, of large clear angular cells. The internal seminal vesicle occupies the larger part of the interior, while the cirrus is a very narrow straight tube which opens into the small, slender and deep genital atrium just dorsal to the vagina. The external seminal vesicle is an elongate, thin-walled structure which is to be found anterior to and between the two poral testes. The testes have functioned and are found to be disappearing in proglottids about 50 mm from the scolex. The pore is to be found on the right hand border in the anterior one-third of the lateral margin.

The start of the ovary is to be found in proglottids about 35 mm from the scolex in the form of a transversely elongated structure with a few small lobes on the anterior border. As development proceeds, it elongates transversely and the lobes increase in number and depth so that in proglottids about 50 mm from the scolex, the organ has the outline and extent as indicated in figure 38. The vitelline gland is situated posterior to the ovary and is a transversely elongated oval organ but slightly lobed. The vagina is at first a clearly differentiated, thin-walled duct which leads at first almost directly medially, then posteriorly ventral to the poral testes, then posterior to the median testes to the region of the beginnings of the ovary and vitellaria. Its inner end is slightly wider than the remainder of its length and becomes widely expanded into a seminal receptacle. Its entire length serves, however, as a reservoir for the spermatozoa, since it becomes a wide tube and completely filled with them. Its course when filled with the spermatozoa in the mature proglottids is very irregular and contains several curves. Both the cirrus sac and vagina pass dorsal to the longitudinal excretory vessels. The uterus is a large transverse sac divided irregularly into lobes. The eggs in all the specimens examined were immature. They have but two shells and no hooks could be made out in any that were examined. The space between the shells is filled with a loose cellular mass which appeared to be breaking up in more mature eggs. The embryos are spherical and vary in diameter from 7 to 12 $\mu$  and the shell 18 to 28 $\mu$ . These measurements, however, are not thought to be of much value, especially those of the shell, since they are very much distorted by pressure from adjoining eggs and by shrinkage.

The longitudinal muscles are irregularly placed and all the bundles are of about the same size. Their position varies according to the position

in the proglottid at which the section is selected, being farther from the surface in the posterior than in the anterior. The longitudinal nerve lies about midway between the large excretory vessel and the border of the proglottid. The dorsal excretory vessel is 26 by  $10\mu$  in proglottids about 35 mm from the scolex, while the ventral is much larger, being 21 by  $8\mu$  size in the same region. No connections could be found between the ducts of the two sides.

Of the species described from the order Pygopodes as listed by Fuhrmann (1908), *H. capillaris* deserves some discussion. The shape of the rostellum is apparently flat as figured by Krabbe (1869) and not lobed. The hooks as figured by Krabbe are different in shape, the basal part being much more curved and the blade more bent, although the size as given by Krabbe is  $15\mu$ . The position of the testes and ovary is not well understood. The hooks of *H. furcifera* (Krabbe 1869) are 26 to  $33\mu$  in length and much different in shape, the blade being much longer, heavier, and the base more curved than found in the species described above. *Wardium capillaroides* Fuhrmann (1906: 355) from *Podiceps dominicus* (L.) has two of the testes on the antiporal side, the farther one somewhat variable in position but usually in a transverse row. The hooks of this species are larger ( $21\mu$ ) and much more slender in structure in all parts than in the above described species. *H. podicipina* Szymanski 1905 has much smaller testes which are arranged two antiporal, one of which is in front of and ventral to the other. The hooks have much heavier basal parts and about three times as long (42 to  $46\mu$ ) as in the new species described above.

Of the species which have the testes sufficiently well described to determine their location, *H. brevianmulata* (Fuhrmann 1906c) deserves mention. The testes, however, are much smaller, being 0.04 mm in diameter while in the species described above they are about 0.25 mm long and 0.15 mm wide. The ovary is median and although not stated is presumably ventral to the median testes while in our species it is mainly between the two testes on the side away from the pore. The scolex was absent from Fuhrmann's species. The other species which are related to the above described form by having the testes in a transverse row, are all markedly different in the shape and size of the hooks, ovary, and cirrus.

#### HYMENOLEPIS CUNEATA N. SP.

[Figs. 48-53]

The specimens forming the basis of the description of this species were obtained from a wild duck killed at Table Rock, Nebraska, on June 22, 1896, and are preserved in the collection of H. B. Ward.

Of these specimens the following mounts, consisting of eight totos and five sets of serial sections, numbers 25.14 to 25.20 inclusive, were desig-

nated as cotypes. They remain in the Ward Helminthological Collection at the University of Illinois, Urbana.

*External Anatomy.* The specimens of this species vary from 30 to 40 mm in length, those of about 30 mm usually lacking eggs in the uterus but have the female organs well developed. The shape of the strobila is peculiar in that the widest part is usually from 3 to 5 mm from the posterior end, and tapers gradually toward the scolex, the general form thus being wedge-shaped. Specimens vary from 3 to 4 mm wide at the widest point and from 0.5 to 1 mm wide at the central part of the strobila. The posterior portion is evenly rounded behind the widest part, and the last proglottid is sterile and much smaller than those immediately in front. Strobilae 30 to 35 mm long have from 200 to 250 proglottids while those about 40 mm long have about 300. The genital pores are unilateral and on the right side of the proglottid. No irregularity in the structure of the genital organs or the general structure of the proglottids has been observed.

The scolex is a strongly developed structure, measuring about 0.35 mm in diameter, and carrying four suckers, each of which are about 0.15 mm in diameter. The rostellum is provided with a sac which occupies about one-third the diameter of the scolex. The rostellum is a solid muscular organ of about the same diameter throughout its entire length, and is not retracted into the rostellar sac as an introvert. It carries from six to eight very sharp and strong hooks arranged in a single row about its distal end. Two specimens were found to possess six hooks, one had seven, and three had eight, so it is evident that the number is by no means constant. The hooks are large enough and placed far enough apart so that there is little difficulty in making an accurate count. They vary in length from 103 to 115 $\mu$ , the majority measuring from 105 to 108 $\mu$ ; only four were found which measured 112 and 115 $\mu$ .

The three testes lie in a transverse row in the center of the proglottid and are about equally spaced. They are somewhat oval and measure about 500 $\mu$  along the transverse diameter of the proglottid, 170 $\mu$  dorsoventrally, and about 100 $\mu$  antero-posteriorly in proglottids about 22 mm from the scolex. The larger part of the ovary is found anterior to and on the antiporal side of the middle testes. It occupies the larger part of the central region of the proglottid when fully developed. The vasa efferentia arise on the median side of the two lateral testes and on the dorsal side of the median testes. The ducts from the two poral testes join, and the short common duct thus formed unites with the vasa efferentia from the antiporal testes. The vas deferens soon communicates with the external seminal vesicle at its median end. The latter communicates with the internal seminal vesicle through the slightly coiled remaining portion of the vas deferens, which lies dorsal and anterior to the poral testis. The external seminal vesicle lies dorsal and anterior to the region between the two poral testes.

The cirrus sac lies dorsal to the excretory ducts as does the vagina. A rather large and somewhat dumb-bell shaped internal seminal vesicle occupies about three-fourths of its inner portion and communicates with the cirrus by means of a wide duct. The vas deferens communicates with the internal seminal vesicle at its inner end, which lies against the wall of the sac, and the duct leading to the cirrus arises at the end of the vesicle nearest the pore. The latter passes back alongside the vesicle to the inner enlarged end where it enters the cirrus. The cirrus extends inward about three-fourths the length of the sac and lies along one side of the wall for the greater part of its length. It is usually straight but in some instances is slightly bent or coiled in parts, and is provided with hooks only along its outer portion. The vagina opens ventrally and somewhat posteriorly to the cirrus into the genital atrium. The latter varies much in depth in different parts of the strobila. The total length of the internal seminal vesicle is about  $500\mu$ , the width of the inner enlargement 60 to  $75\mu$ , and of the outer 50 to  $60\mu$  in proglottids about 22 mm from the scolex. The cirrus sac is about 1 mm in length in this region.

The beginnings of the ovary and other female reproductive organs appear in proglottids about 20 mm from the scolex, and are fully developed about 30 mm from the scolex. The ovary is deeply divided into 15 to 20 irregular rounded lobes, and lies anterior and ventral to the median testes occupying the middle one-third of the proglottid. The vitelline gland is likewise lobed and lies in the concavity in the posterior side of the ovary. The ootype is rounded and is located ventral to the vitelline gland.

The vagina opens on a well marked papilla which is ventral and anterior to the opening of the cirrus sac. The two do not usually open on the same level, but the vagina into a deep depression of the genital atrium extending back along the cirrus sac. The lateral portion of the vagina is a narrow duct which lies close to the cirrus sac and the vas deferens until it widens out to form the thin-walled seminal receptacle. The latter is found just beyond the seminal vesicle and about on the same level in young proglottids. The duct leading from it to the region of the female reproductive organs can be traced. As development proceeds, almost the entire median portion of the vagina becomes distended by spermatozoa, forming a very large seminal vesicle extending almost to the excretory vessels, and occupying the larger portion of the central region between the muscular layers in proglottids about 30 mm from the scolex. The seminal receptacle is first evidenced by a slight widening of the duct just beyond the seminal vesicle, and as development proceeds, this widening is found to extend along the duct toward the pore, and in mature proglottids this whole portion of the duct becomes filled with spermatozoa as described above.

The uterus is a sac-like structure, which extends, on either side beyond the excretory vessels, and fills the larger part of the ripe proglottids. It is

deeply divided into irregular lobes by septa. The eggs, in every specimen examined, were found to be very immature, being only rounded or oval masses of cells and showing no shell.

The longitudinal muscles are very well developed and are in two irregular layers on either side of the proglottid. The outer one has the bundles usually of a smaller size than those of the inner, though some are as large as those of the inner layer. No oblique muscle bundles could be located. Two groups of from four to six longitudinal muscle bundles are found on each side of the proglottid, one on either side of the spaces between the testes. Two longitudinal excretory vessels lie on either side of the proglottid, ventral to the vagina and cirrus sac. The larger one is ventral and measures about  $50\mu$  in diameter about  $20\mu$  mm from the scolex. The smaller one is about  $20\mu$  in diameter in the same region, and lies invariably directly dorsal to the larger. A careful examination of these in sections failed to reveal any transverse ducts joining those on opposite sides of the proglottid.

A comparison of this species with others is indeed difficult, because there has been no description found which shows a similar combination of characters. When compared with the other species which have the testes arranged in a transverse row, none are found which show any resemblance to it. Likewise when the hooks are compared, there are no others which have such large ones of a similar shape and number except *H. macracanthos*, v. Linstow 1877, but these are different in that there is no projection on the posterior basal portion. This species was described from an immature specimen and consequently could belong to any one of several genera as pointed out elsewhere in this report.

When the descriptions of the species that have been found in Anseriformes are compared, no one is found which compares with it in size and shape of hooks and arrangement of the internal organs. It seems proper to conclude therefore that this form is an undescribed species.

#### HYMENOLEPIS SACCIPERIUM N. SP.

[Figs. 40-47]

The material which formed the basis for the following description was taken from the intestine of two specimens of *Marila marila*, American scaup duck, or bluebill, one of which was killed at Peoria, Illinois, November 25, 1923, and the other at Lincoln, Nebraska, April 11, 1908. The specimens from the host taken at Peoria, Illinois, are in the collection of the author under the number 584a, and are designated as cotypes. In the Ward Helminthological Collection at the University of Illinois, Urbana, there are eight mounts, five totos and three sets of serial sections, numbers 25.21 to 25.26 inclusive. These were prepared from the specimens taken at

Lincoln. The type is No. 25.21 in the Ward Collection of Parasites at Urbana.

*External Anatomy.* The length of specimens which have well developed eggs in the posterior proglottids is about 38 cm. The width increases gradually from  $150\mu$  immediately behind the scolex to the greatest width, 1.25 mm to 2 mm, 9 to 10 cm from the scolex. Throughout the greater part of the remainder of the strobila, the width is about the same, but decreases slightly toward the posterior end. The above measurements are for specimen No. 584a3. The proglottids are about  $35\mu$  long at about 35 mm from the scolex. They increase to  $160\mu$  60 mm from the scolex, while posterior proglottids with well filled uteri measure 1.7 mm wide by 0.32 mm long in larger specimens. The suckers are  $60\mu$  wide, inconspicuous, and but slightly raised above the surface of the scolex.

The scolex is rounded and not conspicuously set off from the neck region behind. It is 0.2 mm wide, while the width of the neck region is about 0.15 mm at its center. The rostellum is short in proportion to the width of the scolex, being about  $25\mu$  in length and  $60\mu$  wide. The tip of the rostellum is dome-shaped and bears a single row of hooks about its margin. The hooks are from 18 to 22 in number and are from 14 to  $17\mu$  long and have the shape indicated by figure 43. The neck region is short, strobilization being evident 1.3 mm behind the scolex by slight constrictions in the surface of the strobila.

The testes are the most conspicuous structures in the entire proglottid. They lie in a transverse row, occupy almost the entire space between the muscular layers, and extend antero-posteriorly almost the full length of the proglottid. The number varies from one to four, about 93 to 95 per cent of the proglottids having three, while in the remainder there are one, two, and four, one being much rarer than any of the other numbers. The arrangement of these with reference to the ovary, vitelline gland and shell gland is likewise very variable; in those proglottids with four testes, three of this number are either on the antiporal side and one on the poral, or two may be on each side, but never three on the poral side; of those having three, two may be on the poral or antiporal side or all three may be on the antiporal side, but never all on the poral; in cases where there are two testes, both may be on the antiporal side, or one may be on either side of the ovary, the latter being slightly more frequent than the former. Proglottids which have one, have this testis on the poral side in the few instances observed. The testes vary much in size and shape in different proglottids, but they are about 0.2 mm in diameter in proglottids while the ovary is about that size. The testes are frequently lobed or deeply constricted usually in the longitudinal axis of the strobila.

The vasa efferentia arise on the anterior, poral side of the antiporal testes and on the anterior antiporal side of the poral testes in those proglottids having three testes. The duct from the farthest antiporal testes

passes anterior and slightly ventral to the median testes and uniting with the one from the latter forming a duct which joins the vas deferens from the poral testes about midway between the poral and the median testes. Considerable irregularity has been observed in these ducts, as is indicated in figure 5, but this seems to be confined to the region where they pass into the vas deferens. These irregularities in the testes occur in the material from both hosts. The vas deferens thus formed then passes to the external seminal vesicle in an almost straight line.

The cirrus sac is about 0.3 mm long and extends medially and anteriorly from the pore which lies about the center of the margin of the proglottid on the right hand side. The internal seminal vesicle occupies about the inner half of the sac, while the cirrus with its attached muscles and associated cells occupies the outer half. The cirrus is a straight tube in most instances but is sometimes slightly coiled. So far as could be observed, it is without hooks. The external seminal vesicle lies anterior to the poral testis and is an elongate structure with thin walls. It is joined to the internal seminal vesicle by a slightly coiled duct. The longitudinal excretory ducts lie beneath the inner end of the cirrus sac and the outer end of the vesicle.

The ovary is a crescent-shaped organ lying usually in the center of the proglottid, but may be somewhat to the right or poral side, when there are three testes on the antiporal side. It is but slightly lobed or indented, and has the somewhat lobed vitelline gland lying in the hollow of the crescent behind. The ootype, and female genital ducts lie between the vitellaria and ovary and somewhat ventral to both. The seminal receptacle is the wide, thin-walled, somewhat coiled portion of the vagina which lies anterior and medial to the poral testes. It is widely distended with spermatozoa in proglottids which have the female organs well developed. The vagina is a wide duct leading from its outer end to its point of opening into the genital atrium ventral to the opening of the cirrus. It lies ventral to and along the posterior side of the external seminal vesicle and ventral to the cirrus sac; in the region of the latter it is usually somewhat bent.

The uterus passes dorsal to the excretory vessels on either side, bends ventrally, passing ventral to the testes, and dorsally again above the ovary, vitelline and shell glands. In the ripe proglottids the uterus occupies almost the entire proglottid. It is slightly lobed or indented on both margins and has the remnant of the seminal receptacle lying in a cavity in its anterior right-hand margin. The number of eggs which the uterus contains varies considerably in different proglottids, some having only a few while others are packed. The eggs were mature in specimens from both hosts, and were essentially the same size. The shells are relatively thick and each of the outer ones were observed to have nuclei within as indicated in figure 42. The middle shell averages 33 by 28 $\mu$  in size with a maximum length and width of 37 by 32 $\mu$ , and a minimum of 28 by 12 $\mu$ . The outer shell was so distorted by shrinkage that scarcely any eggs could be found

which had it well enough preserved for measurement. Its size on the one from which the drawing was made was  $40\mu$  in diameter. The embryos possess six slender hooks, and average 28 by  $15\mu$  in size. Their maximum length and width is 32 by  $18\mu$  and their minimum 16 by  $13\mu$ .

There are two pairs of longitudinal excretory vessels running through the lateral portion of the strobila. The ventral vessel on each side is much the larger of the two, being about 53 by  $25\mu$  in size about 55 mm from the scolex, being elongated in the transverse diameter of the proglottid, while the dorsal is but about  $15\mu$  in diameter in the same region. An examination of the walls reveals no indication of transverse vessels connecting the longitudinal vessels in any part of the proglottid. The longitudinal muscles are but weakly developed, there being approximately 100 bundles on both the dorsal and ventral sides of the proglottid. The oblique muscles are conspicuous and well developed. They lie outside the longitudinal and near the surface of the proglottid.

An examination of the descriptions of the species that are sufficiently complete to state the position of the testes reveals none which are comparable in general characters to the one described above. There is no description in which any detailed reference is made concerning the variations in the number of testes. This characteristic is so noticeable in this species that it seems that it would not have escaped the attention of any one who had examined it.

When the literature descriptive of the species found in Anseriformes is examined, the first species to attract one's attention is *Weinlandia coronula* (Dujardin) 1845, which has 20 to 26 hooks 14 to  $19\mu$  long. The hooks are shaped much like those of the species described above, but are somewhat more strongly constructed throughout in all parts. The musculature of the two species is somewhat similar (Wolffhügel 1900) in that the inner longitudinal layer of bundles consists of a relatively few large conspicuous bundles on the dorsal and ventral sides, (six in *W. coronula* and 10 to 12 in our species on either side) and two or three bundles above and below the excretory vessels near the margin of the worm. The cirrus sac, cirrus, external and internal seminal vesicles, and location of the female reproductive organs are very similar. The outstanding difference, however, is found in the position of the testes. Fuhrmann (1906: 733) says that the two antiporal testes are arranged so that one is anterior and median in position with reference to the other, and Meggitt (1920: 307) says that in the extended specimens studied by him, they have this position though in strongly contracted ones the three may lie in a straight line, yet there is always a small projection of the outer testes lying behind the inner so that there is always a distinction into anterior and posterior testes. The other species found in the Anseriformes having the hooks similar in number and length have no resemblance to the above described form in internal structure. It seems justifiable, therefore, to designate this form as a new species.



## GENUS WEINLANDIA NOV. GEN.

Three testes in a proglottid, two located on the posterior border and the third directly anterior, anterior and median, or anterior and lateral to the antiporal posterior testis. Rostellum generally well developed and armed or unarmed. Vas deferens with an internal and an external seminal vesicle. Genital ducts dorsal to the longitudinal excretory vessels or exceptionally between or below. Pores unilateral.

Type species: *Weinlandia macrostrobilodes* n. sp.

## LIST OF THE SPECIES OF WEINLANDIA

*Two testes posterior, the third anterior and lateral to the posterior antiporal testis.*

1. *Weinlandia arcuata* Kowaleski 1905.  
See Kowaleski 1905: 222-238; 1905a: 532-533 (Figs. 1-9).
2. *Weinlandia cyrtoides* n. sp.  
See this paper, p. 59.
3. *Weinlandia abortiva* von Linstow 1904.  
See von Linstow 1904a: 383 (*Hymenolepis voluta*): 1905: 362.
4. *Weinlandia chionis* Fuhrmann 1921.  
See Fuhrmann 1921: 517-518 (Figs. 110-113).
5. *Weinlandia collaris* (Batsch 1786) Fuhrmann 1908.  
See Stiles 1896: 40-41 (Figs. 116-146) (*Drepanidotaenia sinuosa*).  
Cohn 1901: 323-325 (*Hymenolepis sinuosa*).
6. *Weinlandia diorchis* Fuhrmann 1913.  
See Fuhrmann 1913: 29-31 (Figs. 21-25).
7. *Weinlandia farciminosa* (Goeze 1782).  
See Krabbe 1869: 321-322 (Figs. 230-232) (*Taenia farciminalis*).  
Volz 1900: 32-35 (Fig. 10) (*Diplacanthus farciminalis*).
8. *Weinlandia flagellata* Fuhrmann 1906.  
See Fuhrmann 1906b: 356-357 (Figs. 8-9).
9. *Weinlandia globocephala* Fuhrmann 1918.  
See Fuhrmann 1918: 443-445 (Figs. 64-66).
10. *Weinlandia gracilis* (Zeder 1803) Cohn 1901.  
See Stiles 1896: 38-39 (Figs. 80-99) (*Drepanidotaenia gracilis*); Wolffhügel 1900: 176-183 (Figs. 106-109) (*D. gracilis*); Cohn 1901: 327-329; Clerc 1903: 305-306 (*D. gracilis*).
11. *Weinlandia glandularis* Fuhrmann 1909.  
See Fuhrmann 1909: 43-44 (Fig. 42).

12. *Weinlandia jaegerskioeldi* Fuhrmann 1913.  
See Fuhrmann 1913: 25-26 (Figs. 15-17).
13. *Weinlandia longirostris* (Rudolphi 1809).  
See Krabbe 1869: 293; Fuhrmann 1906: 733.
14. *Weinlandia microsoma* (Creplin 1829) Cohn 1901.  
See Krabbe 1869: 296-298 (Figs. 146-150) (*Taenia microsoma*);  
Cohn 1901: 284-288 (Figs. 15-22); Fuhrmann 1913: 23 (Figs. 12-14).
15. *Weinlandia meleagris* (Clerc 1902) Fuhrmann 1906.  
See Clerc 1902a: 574-575; 1903: 306.
16. *Weinlandia megalops* (Nitzsch in Creplin 1829) Parona 1899.  
See Ransom 1902: 158-167 (Figs. 11-14).
17. *Weinlandia lateralis* n. sp.  
See this paper, p. 56.
18. *Weinlandia papillata* Fuhrmann 1906.  
See Fuhrmann 1906b: 357-358 (Figs. 10-11).
19. *Weinlandia parvula* Kowaleski 1905.  
See Kowaleski 1905a: 533-534 (Figs. 10-17).
20. *Weinlandia rara* Skrjabin 1914.  
See Skrjabin 1914: 468.
21. *Weinlandia stylosa* (Rudolphi 1810) Volz 1899.  
See Krabbe 1869: 326 (Figs. 242-244) (*Taenia stylosa*). Volz 1900:  
141-144 (Fig. 9) (*Diplacanthus stylosus*).
22. *Weinlandia styloides* Fuhrmann 1906.  
See Fuhrmann 1906: 354 (Figs. 3-5).
23. *Weinlandia sphenoccephala* (Rudolphi 1809).  
See Fuhrmann 1906: 449 (Figs. 34-35).
24. *Weinlandia serpentula* (Schränk 1788) Weinland 1858.  
See Volz 1900: 135-140 (Fig. 8) (*Diplacanthus serpentulus*); Cohn  
1901: 294-297 (Figs. 23-25); Clerc 1903: 295-296 (Fig. 8) (*Drepani-  
dotaenia serpentulus*).
25. *Weinlandia tritesticulata* Fuhrmann 1906.  
See Fuhrmann 1907a: 531-532 (Figs. 34-36).
26. *Weinlandia teresoides* Fuhrmann 1906.  
See Fuhrmann 1906c: 443-444 (Fig. 20).
27. *Weinlandia vaginata* Baczyńska 1914.  
See Baczyńska 1914: 214-218 (Figs. 49-50).

*Two testes posterior, the third anterior to the antiporal posterior  
testis.*

28. *Weinlandia annandalei* Southwell 1922.  
See Southwell 1922: 374-377 (Figs. 10-13).
29. *Weinlandia amphitricha* (Rudolphi 1819) Fuhrmann 1906.  
See Krabbe 1869: 311-312 (Figs. 195-197) (*Taenia amphitricha*); Clerc  
1903: 293-295 (Fig. 21) (*Drepanidotaenia amphitricha*).

30. *Weinlandia brevis* Fuhrmann 1906.  
See Fuhrmann 1906e: 753-754 (Fig. 22).
31. *Weinlandia columbina* Fuhrmann 1909.  
See Fuhrmann 1909: 41-42 (Fig. 38-40).
32. *Weinlandia caroli* Parona 1887.  
See Fuhrmann 1906e: 741-743 (Fig. 3-7).
33. *Weinlandia carioca* (Magalhaes 1898) Ransom 1902.  
See Ransom 1902: 151-158 (Fig. 1-10); 1905: 274-276 (Figs. 3, 10, 22, 28); Guberlet 1919: 35-38.
34. *Weinlandia corvi* n. sp.  
See this paper, p. 62.
35. *Weinlandia interrupta* (Rudolphi 1802) Fuhrmann 1906.  
See Fuhrmann 1906e: 745-746.
36. *Weinlandia intermedia* Clerc 1906.  
See Clerc 1906: 436 (Figs. 7-9).
37. *Weinlandia inflata* (Rudolphi 1809).  
See Cohn 1901: 330-331.
38. *Weinlandia importata* Fuhrmann 1918.  
See Fuhrmann 1918: 447-449 (Fig. 75-78).
39. *Weinlandia ibidis* Johnston 1911.  
See Johnston 1911: 88 (Figs. 22-24).
40. *Weinlandia liguloides* (Gervais 1847).  
See Fuhrmann 1906e: 741-745; Cohn 1901: 271-277 (Figs. 1-5).
41. *Weinlandia lobata* Fuhrmann 1906.  
See Fuhrmann 1906b: 352-353 (Fig. 1).
42. *Weinlandia megalorchis* Lühe 1898.  
See Cohn 1901: 277-280 (Fig. 6-12).
43. *Weinlandia medici* (Stossich 1890) Fuhrmann 1906.  
See Fuhrmann 1906e: 749-750 (Figs. 14-16).
44. *Weinlandia microscolecina* Fuhrmann 1906.  
See Fuhrmann 1906e: 740.
45. *Weinlandia magniovata* Fuhrmann 1918.  
See Fuhrmann 1918: 445-447 (Figs. 68-72).
46. *Weinlandia octacantha* (Krabbe 1869) Fuhrmann 1906.  
See Krabbe 1869: 301 (Fig. 162) (*Taenia octacantha*); Fuhrmann 1906e: 746-747 (Figs. 9-10).
47. *Weinlandia phasianina* Fuhrmann 1907.  
See Fuhrmann 1907a: 533-534 (Figs. 40, 41).
48. *Weinlandia passerina* Fuhrmann 1907.  
See Fuhrmann 1907a: 533 (Fig. 39).
49. *Weinlandia parina* Fuhrmann 1907.  
See Fuhrmann 1907a: 534 (Fig. 42).
50. *Weinlandia pellucida* Fuhrmann 1906.  
See Fuhrmann 1906c: (Figs. 12-13).

51. *Weinlandia planestici* n. sp.  
See this paper, pp. 73-75.
52. *Weinlandia rostellata* (Abildg. 1793).  
See Fuhrmann 1895: 443-449 (Fig. 5-10) (*Taenia capitellata* Rud.)
53. *Weinlandia simplex* Fuhrmann 1906.  
See Fuhrmann 1906e: 753 (Figs. 20-21).
54. *Weinlandia tetracis* Cholodkovsky 1906.  
See Cholodkovsky 1906: 338-339 (Figs. 18-21).
55. *Weinlandia tubicirrosa* Baczynska 1914.  
See Baczynska 1914: 217-218 (Figs. 49-50).
56. *Weinlandia tenuis* Clerc 1906.  
See Clerc 1906a: 536-537 (Figs. 19-21) (*Echinocotyle tenuis*).
57. *Weinlandia uncinata* Fuhrmann 1906.  
See Fuhrmann 1906c: 441 (Figs. 14-15).
58. *Weinlandia zosteropis* Fuhrmann 1918.  
See Fuhrmann 1918: 441-443 (Fig. 59-63).

*Two testes posterior, the third anterior and median to the  
antiporal posterior testis.*

59. *Weinlandia armata* Fuhrmann 1906.  
See Fuhrmann 1906b: 353-354 (Fig. 2).
60. *Weinlandia coronula* (Dujardin 1845) Cohn 1901.  
See Krabbe 1869: 317-318 (Figs. 216-219) (*Taenia coronula*); Stiles 1896: 33 (Figs. 21-28) (*Dicranotaenia coronula*); Wolffhügel 1900: 165-175 (Figs. 97-105) (*Dicranotaenia coronula*); von Linstow 1905: 5 (Figs. 16-18) (*H. megalhystera*), Fuhrmann 1906e: 733; Meggitt 1920: 307-308 (Figs. 1-2).
61. *Weinlandia introversa* n. sp.  
See this paper, pp. 67-70.
62. *Weinlandia interrupta* Clerc 1906 (Name preoccupied, see 35 above).  
See Clerc 1906: 435 (Figs. 5-6). Also listed as 68 below.
63. *Weinlandia macrostrobilodes* n. sp.  
See this paper, pp. 65-67.
64. *Weinlandia microps* (Diesing 1850) Fuhrmann 1906.  
See Wolffhügel 1900: 191-192 (Fig. 110); Fuhrmann 1906e: 733.
65. *Weinlandia querquedula* Fuhrmann 1913.  
See Fuhrmann 1913: 515-517 (Figs. 103-109).

*Two testes posterior, the third anterior to but varying from a  
lateral to a median position with reference to the antiporal pos-  
terior testis.*

66. *Weinlandia asymetrica* Fuhrmann 1918.  
See Fuhrmann 1918: 439-441 (Fig. 53-58).

67. *Weinlandia microcirrosa* n. sp.  
See this paper, pp. 70-72.
68. *Weinlandia interrupta* Clerc 1906  
See Clerc 1906: 435 (Figs. 5-6). Also listed as 62 above.

## DESCRIPTIONS OF NEW SPECIES

### WEINLANDIA LATERALIS N. SP.

[Figs. 55-62]

The specimen which forms the basis of this description was collected by the writer at San Juan Island, Washington, July 7, 1923, from the intestine of *Larus glaucescens* Naumann, glaucous-winged gull, and is preserved in the author's collection under the No. 277.1. Its length is 25 cm and its greatest width 1.6 mm. The anterior portion is very much attenuated, the width just back of the scolex being  $100\mu$ , while 100 mm behind it is but  $136\mu$ . From this point on, it rapidly increases in size as is indicated by the following measurements: 60 mm from the scolex  $220\mu$ , 100 mm from the scolex  $765\mu$ , and near the posterior end 1.6 mm in width. There is scarcely any neck since the slight constrictions indicating the beginning of strobilization are evident immediately behind the scolex. The length of the anterior proglottids about equals the width, but after the sex organs begin to develop, the width rapidly increases in proportion to the length, as is indicated by the following figures: at 40 mm behind the scolex the length about equals the width, namely  $136\mu$ , at 60 mm behind the scolex where the width is  $220\mu$ , the length is  $170\mu$ ; at 100 mm, width  $765\mu$ , length  $255\mu$ ; and in the posterior portion where the width is 1.6 mm, the length is 0.5 mm. The genital pores are unilateral and on the right side in all portions except at a point about 60 mm from the scolex where there are two proglottids which have the pores on the opposite side.

The scolex is but little wider than the anterior end of the strobila, and with the suckers, measures but  $160\mu$  in diameter. The suckers are round and measure  $75\mu$  with an opening  $50\mu$  in diameter. The rostellum, which is fortunately fully extended in the single specimen obtained, is relatively large when compared with the scolex proper. It is  $250\mu$  long with a width at the narrowest part of  $26\mu$ , and at the distal end of  $47\mu$ . The distal end is somewhat dome-like in shape and carries eight hooks which have a shape like figure 55 and which are 26 to  $30\mu$  in length. A little below its center the rostellum has a slight constriction which suggests that this is the point to which it is retracted.

The three testes are all on the poral side of the proglottid, the two nearest the pore are dorsal and on the posterior margin, while the third is somewhat anterior to the median testes and in front of the ovary. The latter is also usually more ventral in position than the other two. Occasion-

ally proglottids appeared to have four testes in toto mounts, but none were observed in sections to have more than three. Testes are often observed to be lobed in sections and this is believed to account for the appearance of four of these organs in toto mounts. The testes are oval or spherical in shape. They measure about  $200\mu$  in length by about  $80\mu$  in width in proglottids 120 mm from the scolex.

The vasa efferentia arise on the sides of the testes nearest the external seminal vesicle, and are very slender ducts. Those from the two antiporal testes unite forming a common duct which is soon joined by the duct from the other testes. No irregularities in the vasa efferentia were observed, although it is not at all unlikely that such occur since the organs are so closely packed together in that region it is very difficult to get any clear idea of their arrangement in many proglottids. The vas deferens, thus formed, is short and soon empties into the external seminal vesicle on its inner margin. The external seminal vesicle is a relatively thin-walled sac which lies just in front of, partly dorsal, or partly ventral to the antiporal testis, and communicates with the cirrus sac through a very small pore. The cirrus sac is one of the most conspicuous structures of the proglottid. It extends about half way across the proglottid and has a well developed retractor muscle extending from its inner end to the wall of the proglottid. Two portions are easily distinguishable, even in toto mounts; the innermost portion contains the internal seminal vesicle and the outer portion contains the cirrus. The internal seminal vesicle is rounded and is divided by partial septa into several almost complete divisions varying in number up to six. These septa seem to disappear as the vesicle becomes enlarged toward maturity, since they are less numerous and even none are present in the proglottids with well developed female organs.

The cirrus is almost straight but is usually more bent and curved along its inner portion than along the outer. The inner portion is also sometimes expanded into a seminal vesicle-like structure. The inner walls of the outer portion especially are thickly set with stout spines. The cirrus sac opens dorsal to the opening of the vagina, and on the right side of the proglottid. Sections at about 100 mm from the scolex show a direct connection between the cirrus sac and the vagina suggesting that self-fertilization is at that time possible (Fig. 59). However, there are no spermatozoa evident at this time and in fact, there is considerable doubt if any are present in the entire strobila. On the other hand, there are numerous eggs undergoing development, as well as single-celled ova, in the uterus of ripe proglottids, which suggests parthenogenesis. In proglottids with well developed female organs there is no genital atrium as the two pores lie side by side on the surface at the border of the proglottid.

The vagina, like the cirrus sac, is a conspicuous organ, reaching about one-third the width of the proglottid or about to the inner end of the cirrus.

The wall of the outer portion is relatively thick, and its inner portion bends ventrally somewhat just medial to the excretory vessels, being rounded and somewhat enlarged. It, like the cirrus sac, passes dorsal to the excretory vessels, and its opening is ventral to that of the cirrus. The median portion of the vagina is a small, somewhat curved duct which passes from the rounded inner end of the thick-walled portion described above, ventral to the testes and dorsal to the ovary to the region behind the antiporal testes where it abruptly enlarges, forming a thin-walled seminal receptacle. A small duct leads ventrally and laterally to its place of union with the oviduct.

The ovary is deeply divided into eight to twelve finger-like lobes, and lies in the posterior left hand portion of the proglottid. The vitelline gland is likewise deeply lobed, and lies in the concavity in the posterior side of the ovary, while the shell gland is rounded and ventrally placed beneath the vitelline gland. The uterus passes dorsal to the excretory vessels on both sides, and dorsal to the ovary, but ventral to the testes. Its start is found in proglottids about 100 mm from the scolex where its course may be traced by a strand of deeply staining cells. In mature proglottids the uterus extends almost to the margins of the proglottids, and is deeply divided into about a dozen irregular lobes. The eggs are immature. They only consist of an oval mass of cells with readily staining nuclei and a clearly defined outer shell. The shell of the largest egg measured was 21 by 16 $\mu$  in size, while the smallest was 16 by 12 $\mu$ . The size of the largest embryo was 16 by 12 $\mu$ , while the smallest was 10 by 11 $\mu$ .

There are two excretory vessels on either side of the strobila, a large ventral one which measures about 75 $\mu$  in diameter at about 100 mm from the scolex, and a small dorsal one about 15 $\mu$  in diameter in the same region. In the anterior and posterior portions of the proglottids, they lie in the central part of the parenchyma about 150 $\mu$  from the margin. Those on the poral side, however, are displaced ventrally in the central portion of the proglottid by the large cirrus sac and vagina. No connecting vessels could be located in either transverse or frontal sections. The longitudinal muscles are in two layers, each of which contains about 30 bundles on each side of the proglottid. The bundles are very variable in size but those of the inner layer are in general, although not always, larger than those of the outer.

This specimen seems to be unique when the literature is examined with reference to the arrangement of the testes and ovary. *H. ardeae* Fuhrmann (1906: 451) has the three testes in a transverse row on the anterior side of the proglottid and the ovary on the side away from the pore beyond the farthest testis. *H. elongata* Fuhrmann (1906: 450) has the three testes in a transverse row on the poral side but in the posterior portion. The following species are similar to the above described species in that the three testes

are all on the poral side of the proglottid: *H. setigera* (Frölich) 1789, *H. venusta* Rosseter 1897, *H. bilateralis* v. Linstow 1905, and *H. lanciolata*, but no one of them has the antiporal testes placed toward the anterior border of the proglottid.

Fuhrmann (1908) lists four species of *Hymenolepis* as occurring in Lariformes. *H. fusa* was described by Krabbe (1869: 307) from *Larus glaucus* from Greenland and *Larus ridibundus* from Bavaria. He records the length as being 250 mm, width 1 mm, 10 hooks 15 to 17 $\mu$  long, and a few other external details, but as is often characteristic of his descriptions, nothing of the internal structure is given. No record has been found of a restudy of the material, but this could not be our species, since the hooks are only about one-half as long and entirely different in shape. *H. baschkiriensis* Clerc 1902, from *Larus canus*, has hooks 73 $\mu$  or more than twice as long as our species, and the cirrus sac is much smaller, being only about one-tenth the width of the proglottid, while in the one described above, it is at least one-half the width. *H. octacanthoides* Fuhrmann 1906 has the testes arranged as in the above description but the ovary and shell gland in the center of the proglottid and anterior to the testes. The fourth species recorded from this group of birds is *Weinlandia microsoma* which has the testes arranged similar to the above, but the ovary occupies the entire posterior portion of the proglottid ventral to the testes, as described by Cohn (1901: 284). There are ten hooks about twice the size of the *W. lateralis*.

#### WEINLANDIA CYRTOIDES N. SP.

[Figs. 85-90]

The material which formed the basis of the following description was obtained from the intestine of *Erismatura jamaicensis*, the Ruddy duck, at Peoria, Illinois, on November 26, 1923. These small cestodes were present in large numbers (about 200) in the single host from which they were obtained. They are preserved in the author's collection under the number 576b.

*External Anatomy.* This interesting little cestode is from 3 to 10 mm in length, depending upon the stage of maturity and the state of contraction of the specimens. The scolex and rostellum are relatively large for the size of the strobila. The rostellum is about 80 $\mu$  long with a knob-like distal end 60 $\mu$  in diameter, and a narrower middle portion 35 $\mu$  long. The scolex is about 0.15 mm wide, and has four rounded suckers about 70 $\mu$  in diameter. The rostellum is armed with eight large dagger-like hooks (Fig. 86), 67 to 70 $\mu$  in length. It is retracted as a solid muscular body and does not seem to be drawn into a sac but only capable of being drawn down toward the scolex, the points of the hooks being drawn down close to its surface.



Strobilization begins about 0.07 to .1 mm behind the scolex and very soon the strobila is well marked off into distinct proglottids. The proglottids are about 0.07 mm wide at the narrowest part behind the scolex; in the region of the thirtieth proglottid about 0.15 mm; at the fiftieth, 0.2 mm; at the sixtieth, 0.4 mm; and at the eighty-fifth, about 0.4 mm. The number of proglottids in a strobila is about 100, the last one is always sterile. The uterus can be found in about the eightieth proglottid, and from there on gradually increases until in the more posterior ones it occupies almost the entire interior. The beginnings of the testes can be made out in the region of the fiftieth proglottid, and the ovary in about the seventy-fifth. The strobila is usually more or less curved toward the poral side of the chain, depending upon the amount of contraction, due to the unsymmetrically developed ovary and uterus. It may be bent so much that the posterior end extends across the middle of the chain in cases of extreme contraction.

The three testes are placed so that two of them are on the posterior side of the proglottid and the other in front of the antiporal posterior testes. The position of the anterior antiporal testes varies considerably, but in young proglottids it is invariable anterior and lateral to the posterior antiporal testes. As the cirrus sac increases in size, it and the mesenchyme surrounding it is usually pushed backward so that the three lie in a transverse row. Occasionally a proglottid is found in which it is ventral to the inner end of the cirrus sac and anterior and lateral to other antiporal testes. Still more rarely it lies directly in front of the latter. One proglottid has been found in which only two testes could be identified in a toto mount. The cirrus sac is the first internal organ to appear in the young proglottid, and it shows as a large transverse group of deeply staining cells in the central portion. This develops into the internal seminal vesicle and the inner portion of the sac. Differentiation gradually proceeds outward until the poral side of the proglottid is reached. The walls of the sac are very thick at first and consist of long columnar or almost cuboidal cells which stain very deeply with Ehrlich's acid hematoxylin. As the internal seminal vesicle becomes filled with spermatozoa, these cells gradually lose their staining properties and decrease in size so that the vesicle becomes a thin-walled sac when completely filled with spermatozoa. The internal seminal vesicle, when thus filled, occupies the larger part of the cirrus sac, and has the cirrus attached at its outer end. The cirrus lies along side the internal seminal vesicle (Fig. 88), where it is variously coiled, and finally passes outward to its point of opening upon the surface of the copulatory bulb. The latter is a structure which first appears in young proglottids as a rounded bulb inside the genital atrium, but in old proglottids is found extended through the widely distended pore into a cone-shaped structure from the tip of which the cirrus is extruded. In young proglottids its surface appears to be roughened by circular folds of the clear outer layer.

These are not found in the fully extended structure, and seem to be merely a folding in the outer surface to accommodate the large surface to the small space. The cirrus itself is entirely smooth. The pore is on the right hand side of the proglottid. The inner end of the internal seminal vesicle is connected with the external seminal vesicle by a narrow, thin-walled coiled duct. The external seminal vesicle is large, and extends medially and posteriorly into the central portion of the proglottid.

The first trace of the ovary can be recognized early as a centrally-placed deeply-staining group of cells. As it becomes mature, it comes to lie in two parts, the larger portion consisting of two or three large rounded lobes in the antiporal side of the proglottid and a much smaller poral portion which is generally not lobed. The large antiporal portion may extend considerably beyond the longitudinal excretory vessels, and occupies most of the that side of the proglottids. The vagina opens into the genital atrium, beside the copulatory bulb behind or slightly under the cirrus, and extends medially along the cirrus sac or somewhat beneath. It is a very difficult organ to find on account of its slight differentiation from the surrounding cells, but it may be located even in some proglottids in toto mount. The uterus appears in the region of the eightieth proglottid and rapidly becomes filled with developing ova. In the posterior proglottids, it is widely distended, occupying almost the whole of the posterior of the proglottid, and is generally somewhat larger in the antiporal side than the poral side of the proglottid. This asymmetrical development of the ovary and of the uterus causes the strobila to bend toward the pore side when the muscles strongly contract.

The ova are immature, having but an outer shell, the inner probably being present in some. There are no hooks present. The shell is filled with a loose cellular mass surrounding the embryo which apparently breaks down as maturity is reached. The size of the shell of the largest egg measured was  $35\mu$  long and  $23\mu$  wide, while the largest embryo was 30 by  $14\mu$  in size. The smallest shell was 28 by  $19\mu$  and the smallest embryo 21 by  $14\mu$ . The excretory ducts are ventral to the genital ducts, the larger one is about 5 by  $12\mu$  in diameter, while the smaller  $5\mu$  in diameter in proglottids where the beginnings of the testes and cirrus sac are well differentiated. They are so crowded and flattened by the excessively developed reproductive glands and organs in the posterior proglottids that they are difficult to identify in cross sections. The longitudinal muscles are well developed, the bundles are about all the same size and the layers are very irregular.

From the records of specimens which have the testes similarly placed, it is a little difficult to decide to which pattern *W. cyrtoides* belongs because of the many incomplete descriptions. It was stated that in the young proglottids the testes were invariably arranged two posteriorly, one on

each side of the ovary and the other anterior and lateral to the antiporal testes, but in ripe proglottids they usually were found in a nearly transverse row due to the greatly enlarged cirrus sac. Among those which have the testes arranged in a transverse row, one poral and two antiporal, there are none which have a similar combination of internal characters and hook size and shape that are found as described above. In the group having the testes arranged two posterior and the other anterior and lateral on the antiporal side, *Weinlandia diorchis* Fuhrmann (1913) from *Somateria mollissima* has hooks that are somewhat similar in shape and length, but the basal portion is much longer in proportion to the blade than in that described above. This species is interesting in that the anterior antiporal testes is small and produces no spermatozoa.

Among those species of Hymenolepis which have been found in Anseriformes, the following deserve mention. *H. trifolium* v. Linstow 1905 has three very small testes located near one another in the center of the proglottid, a cirrus sac reaching only about one-half the width of the proglottid and hooks with a much shorter blade in proportion to the length of the base. *H. macrocephala* Fuhrmann 1913 has hooks 57 to 63 $\mu$  while those of this species are about 70 $\mu$ ; there the blade and base are about equal in length while in the above described form the blade is much longer than the base. The other worm is also 3.5 to 4 cm long while the specimen described above is but 3 to 10 mm in length. *Weinlandia gracilis* (Zeder) 1803 has the testes arranged much according to the plan of the above description, but they are much larger and the total length of the specimen is 27 cm. The remaining species found in Anseriformes are all much different in internal structure and shape and size of hooks. It seems proper to conclude, therefore, that this species is new. Another species, which is described as bent toward one margin is *Weinlandia arcuata* Kowalewski 1904, a species which has the same general plan of testes arrangement as that herein described, but the cirrus sac and other organs very unlike as well as the hooks. One margin is described as shortened, resulting in the entire worm being bent somewhat ring-like. That the internal structure is the reason for this is not apparent as the organs are symmetrically figured.

#### WEINLANDIA CORVI N. SP.

[Figs. 79-84]

The material which formed the basis of the following description was taken from the anterior one-half of the intestine of the common crow, *Corvus brachyrhynchos*, one host being killed on each of the following dates, May 2, Nov. 3, and 10, 1923, at Monticello, Ill. It is preserved in the author's collection under the numbers 203b, 499b, and 531a.

The specimens of this species are from 30 to 62 mm in length, depending on the maturity of the specimens. Specimens having widely extending

uteri filled with ova are about 60 mm long and 0.8 mm wide at the widest point. Proglottids about 25 mm behind the scolex are about  $340\mu$  wide, 40 mm behind are about 0.7 mm wide, while at the posterior end of the chain they are about 0.8 mm wide. The length and width, of course, varies greatly with the stage of contraction. The various reproductive organs are well developed in following regions; testes 30 mm, ovary 40 mm, and the uterus is well formed at about 50 mm from the scolex. The genital pores are strictly unilateral, and on the right hand side of the proglottids. The scolex is sharply set off from the strobila by being about three times as wide as the strobila immediately behind, it being about 0.15 mm wide when the suckers are well extended, while the strobila just behind it is 0.05. The suckers are rather prominent when extended but when contracted are inconspicuous and extend scarcely above the surface of the scolex. They are 0.08 mm in diameter on the scolex from which figure 80 was drawn. The rostellum has not been observed in the extended condition, all being more or less retracted. It is retracted as a solid body and not as an introvert as is indicated by the position of the hooks which are outlined in figure 80. There are eight to ten long slender characteristically shaped hooks (Fig. 82). They are  $33$  to  $36\mu$  in length. The basal part is very long as compared with the blade and is usually almost straight but may be either straight or more or less curved.

Two of the three testes are placed on the antiporal side of the proglottid and one in front of the other. The anterior one is usually directly in front of the posterior, but may be lateral, no instance has been observed where it is medial. The poral testes is in the posterior portion of the proglottid in a line with the posterior antiporal one. The vasa efferentia of three proglottids sectioned frontally from the same specimen are shown in figure 4. From these outlines it is observed that they are irregular. The cirrus sac extends considerably beyond the longitudinal excretory vessel. The internal seminal vesicle is relatively small although it occupies somewhat more of the interior of the pouch when fully distended with spermatozoa than is indicated in the early stages (Fig. 83). From its outer end, the cirrus extends in an almost straight line to the opening into the genital cloaca, dorsal to the opening of the vagina. The walls of the cirrus sac and internal seminal vesicle are relatively thick and in some worms the interior contains much loose connective tissue around the vesicle. The genital cloaca is relatively deep.

The external seminal vesicle is found in the central anterior portion of the proglottid in front of and partially dorsal to the ovary. Its connection with the internal vesicle is through a straight or slightly coiled duct. Well developed testes are to be found in proglottids about 30 mm from the scolex while their first traces are seen much farther anterior to this. The internal end of the cirrus sac is to be found in very young proglottids.

The ovary is found to be well developed about 35 mm from the scolex, while its start is easily made out 10 mm farther forward. It is divided indistinctly into two portions by being narrower in the region just anterior to the vitellarium. The antiporal portion is somewhat larger and is sometimes slightly lobed, while the poral portion is not lobed or very indistinctly so. The vitelline gland is ventral and somewhat posterior to the ovary and lies about in the center of the proglottid. The vagina opens ventral to the cirrus, and is a wide tube with large irregular shaped cells in its walls. It widens out rapidly medial to the cirrus sac and in old proglottids is found to be a wide sac dorsal to the ovary and completely filled with spermatozoa. The vagina and cirrus sac pass dorsal to the nerve and excretory vessels and the pore is always on the right hand side of the proglottid. The uterus in the posterior proglottids extends well out to the border, but occupies the posterior portion only since the large cirrus sac and external seminal vesicle lie in the anterior portion. The eggs were not found to be mature in any specimen examined. In well preserved material they were only oval or rounded masses of cells with nuclei of varying sizes. In some proglottids the uterus is almost divided into two lateral portions by the large central seminal receptacle. The longitudinal excretory ducts are relatively large and conspicuous, the large ventral one being 50 by 20 $\mu$  and the smaller 10 $\mu$  in diameter in proglottids about 30 mm from the scolex. The longitudinal muscles are irregular in their arrangement, there being numerous small bundles in the dorsal and ventral portions of the proglottids.

In a discussion of the literature descriptive of cestodes with structures similar to this, the following species deserve mention. In the group of species which have a similar arrangement of testes is *H. arcuata* Kowalewski 1904; here the anterior antiporal testes, however, is lateral to the posterior, the cirrus much smaller, and the hooks, although somewhat similar in shape, are only about half as long as in the above described species. *W. importata* Fuhrmann 1918 has the hooks very slender and with a short blade but with almost no posterior basal portion, the cirrus sac very small and not reaching the excretory ducts, and the two antiporal testes arranged so that the anterior one is lateral to the posterior. *W. interrupta* Fuhrmann (1906: 745) has the position of the two antiporal testes described as being one before the other but not otherwise specific. The hooks have a small blade and small posterior basal portion like in the above described species, but the anterior basal portion is much thicker and stronger. Their length is 27 $\mu$ , somewhat under those described above, and the host belongs to the Charadriiformes, while the crow belongs to the Passeriformes. *W. zosteropsis* Fuhrmann (1918: 441) from *Zosterops minuta*, has many similarities, but yet some rather important differences. The cirrus sac is longer and narrower when the figures of ripe proglottids are compared. The ovary is narrower, and considerably lobed, while in the above described form there

are but few lobes. The testes are smaller (50 to 60 $\mu$  in diameter as compared with 100 $\mu$  in the above species) and the anterior basal portion of the hooks is much larger than in the species described above.

When the literature is examined with reference to the species of *Hymenolepis* found in Passeriformes, *W. pellucida* has a somewhat similar arrangement of the testes, but the poral is widely separated from the antiporal, and the hooks, although of a similar length, are not alike in shape. *W. magniovata* Fuhrmann 1918 has hooks similar in length but not similar to those described above in shape, and the internal structure of the proglottid is very different in that the testes are smaller and widely separated from each other. It seems, therefore, proper to conclude that the species described above is new.

### WEINLANDIA MACROSTROBILODES N. SP.

[Figs. 63-71, 78]

The specimens forming the basis of the following description of this species were taken from the intestine of *Anas rubripes*, the black duck, one host being taken at Monticello, Illinois on November 3, 1923 and another at Beardstown, Illinois, on November 1, 1923. The parasites are preserved in the author's collection under the numbers 498a and 488a.

The length of worms with fully developed uterus is about 15 cm, while the greatest width is 2 to 2.5 mm. The strobila is very slender immediately behind the scolex, being usually less than half a millimeter wide, but rapidly increases beyond the 10 mm point to a maximum 25 mm behind the scolex. The shallow constrictions marking off the proglottids begin to appear about half a millimeter behind the scolex, consequently there is almost no neck. In the older proglottids the posterior border overlaps the anterior portion of the next proglottid a short distance depending upon the state of contraction of the specimen. The genital pores are marginal, on the right hand side, and somewhat in front of the center of the proglottid.

The scolex is relatively very small when compared with the total length and width of the worm. It is about 125 $\mu$ , or but little more than 0.1 mm in diameter in the expanded condition. The rostellum is, on the other hand, rather large in proportion to the scolex. It is about 60 $\mu$  long and 50 $\mu$  in diameter at the distal end. The distal portion is somewhat enlarged, and carries a crown of 20 or 21 small hooks. Of the four scolices obtained, the rostellum of one of these had 20 hooks, two of the others had 21, while the fourth was contracted in such a manner that the hooks could not be counted with certainty. The hooks are of the shape indicated in figure 65 and are 15 to 16 $\mu$  in length. The rostellum is retracted into the somewhat shallow rostellar sac as a solid body. The suckers are conspicuous, strongly developed structures with a diameter of about 70 $\mu$  when expanded. The opening is about 40 $\mu$  in diameter. They are unarmed.

In the male system two of the three testes lie on the posterior side of the proglottid, one on each side of the ovary and vitelline gland. The other testis is anterior and median to the antiporal testes. In an examination of 340 proglottids to determine the regularity of the testes, eight were found which either had less than three testes or an abnormal arrangement. One of these proglottids had two testes on the poral side and one on the antiporal, all in a transverse row, which is suggestive of an ancestral condition in which there were two or more testes on the poral side, while the occurrence of but one on the poral suggests that possibly the two regularly found there have united. In another there are three on the poral side, two of which are much smaller, suggesting that these have not united. The vasa efferentia arise on the median border of the testes and pass medially. Those from the two antiporal testes usually join, forming a common duct which soon unites with the one from the poral testes just median to the seminal receptacle. The vas deferens, thus formed, is a straight tube, and passes anteriorly and laterally near the median wall of the seminal receptacle to the end of the seminal vesicle. The vasa efferentia were found to be somewhat irregular in their arrangement, as will be seen by examining figures 2 and 3. In some proglottids and in one worm in particular from which their arrangement is shown in 7 consecutive proglottids in figure 2, the vasa efferentia are very irregular. From these, it may be observed that the three main efferentia unite usually as described above, that is, the two from the antiporal testes join before uniting with the poral duct, but in proglottid e, they all three unite at the same point. The number of ducts from a single testes is also seen to be very variable, there being from one to four. In another specimen, the manner of joining of the ducts was found to be irregular, but in the few proglottids that were sectioned, no other irregularities were observed.

The seminal vesicle is about 0.25 mm long in proglottids 65 mm from the scolex, it having increased from a slender, deeply staining tube in the anterior proglottids to a widely expanded, elongate bulb with the sexual development and the production of the spermatozoa. Its lateral end reaches to the longitudinal excretory vessels, and is joined with the cirrus sac by a slender duct which passes dorsal to the latter and makes one to four coils in the course of this short distance.

The cirrus sac reaches to the longitudinal excretory vessels and is about 3 mm long. A large internal seminal vesicle occupies about half of its length, and early becomes filled with spermatozoa. The cirrus is a very slender thin-walled tube which can only be traced with high magnifications. Its inner portion and sometimes well out to the outer end, has wavy walls which at the narrow places leave only a very narrow lumen. The outer portion has its wall set with very fine spines.

In the female system the ovary is placed somewhat ventrally and in the posterior half of the proglottid. It consists of about ten slender

lobes directed anteriorly and laterally, joined at their bases by a slender portion of the organ.

The vitelline gland lies posterior to the ovary in the semicircular space bounded anteriorly by the latter. It possesses from four to six rather blunt lobes, and has much the same appearance as the ovary in sections and toto mounts of the younger proglottids but soon can be distinguished from the latter by the smaller nuclei as the ovarian nuclei rapidly enlarge toward maturity.

The seminal receptacle is about 0.3 mm long, and lies bent around the anterior and median border of the poral testis, its rounded inner end reaching almost to the ootype. Its duct is short and uncoiled. The lateral portion lies ventral to the seminal vesicle and reaches almost to the longitudinal excretory vessels, always passing dorsal to the latter, as does the sperm duct, and along the posterior side or somewhat ventral to the cirrus sac to the genital cloaca, into which it opens immediately posterior or somewhat ventral to the cirrus sac.

The outer shell of the eggs varies in length from 23 to 30 $\mu$ , and in width from 17 to 28 $\mu$ , the average size being 21 by 27 $\mu$ . The inner shell is closely applied to the embryo, and the middle usually so close to the outer that there is no appreciable distance between them, but may be easily distinguished where the middle is folded inward. The embryo is on the average 12 by 23 $\mu$  in size, but varies in length from 17 to 25 $\mu$ , and in width from 10 to 16 $\mu$ . The six hooks are about 9 $\mu$  in length and their shape is represented in figure 66.

Here as usual the excretory system of the proglottids consists of two longitudinal vessels in each lateral portion about 0.4 mm from the margin. The ventral vessel is much the larger, being about 120 $\mu$  in diameter while the dorsal is only about 25 $\mu$  in diameter. The small dorsal vessel curves laterad and mediad much more sharply than the larger, and may be as far out as the middle of the internal seminal vesicle. The larger, on the other hand, lies along the margin of the testes and passes almost invariably under the small sperm duct joining the seminal vesicle and sperm sac. No trace of transverse excretory vessels has been observed either in totos or sections.

Because of the great similarity between this form and *W. introversa*, the reader is referred to this section in the description of the latter species for a comparison of the organs.

### WEINLANDIA INTROVERSA N. SP.

[Figs. 72-77]

The material which formed the basis of the following description was obtained from the intestine of two specimens of *Anas platyrhynchos* Linnaeus, the mallard duck, obtained at Peoria, Illinois, November 23 and



25, 1923, preserved in the author's collection under the numbers 577 and 578, and from one specimen of *Anas rubripes*, the black duck, at Monticello, Illinois, on November 3, 1923, and preserved in the author's collection under the number 498a9. But a single specimen was obtained from the latter host along with several specimens of *W. macrostrobilodes*.

The specimens of this species are much like *W. macrostrobilodes* in position of the testes, ovary, and other internal organs, but they can be distinguished with considerable certainty by their smaller size, being only from about one-third to two-thirds as long. The specimens studied were from 50 to 80 mm in length and about 1.5 to 2 mm broad at the widest part. The anterior portion of the strobila is slender, being less than 1 mm wide in the region about 30 mm behind the scolex, but increases rapidly in width and thickness from there on posteriad, the posterior one-fourth to one-half of the strobila being usually of almost uniform width. When the number of proglottids was counted in comparing the position in the strobila where the testes and ovary had reached about the same stage of development as in *W. macrostrobilodes*, it was found that this point was from 300 to 400 proglottids behind the scolex, while in *W. macrostrobilodes* there were only about 300 in any instance. When the distances were compared, in *W. introversa* it was found to be about 25 mm from the scolex, depending on the state of contraction, while in *W. macrostrobilodes* it was 40 to 60 mm. An accurate idea of the comparative width and size of the internal organs may be obtained by comparing figures 68 and 75 which are camera lucida drawings of the same magnification made of the testes and ovary in relatively the same extent of development in the two species. All of the specimens of the two species have been compared with these drawings.

The scolex shown in figure 73 is about 0.2 mm wide when measured across the extended suckers. The latter are 0.08 mm wide and the rostellum 0.05 mm long by 0.07 mm in maximum width. There are 20 hooks 17 to 20 $\mu$  in length, which have the shape indicated in figure 74. When the hooks are compared in number, size, and shape with *W. macrostrobilodes*, it is a striking fact that they are almost identical in every way and the one might easily be mistaken for the other, due to the difficulty of observation or to variations. The rostellum is retracted as an introvert. A drawing of a longitudinal section is shown in figure 72, which shows the arrangement of the musculature. There is a bulb-like mass of muscles and connective tissue attached in the central portion of the tip within the crown of hooks. This permits the hooks to be inverted so that their blades are directed outward when the whole is retracted. This is an entirely different arrangement from that found in the scolex of *W. macrostrobilodes* (Fig. 63).

In the male system, which has been referred to above, the internal organs are almost identical in position and general structure with those of *W.*

*macrostrobilodes* except that they are smaller. The three testes are arranged, one poral and the other two antiporal, one of the latter being in front of and median to the other. They are irregularly lobed by slight indentations about their edges, and have the vasa efferentia arising on their median borders. The vasa efferentia pass medially in each instance, the two from the antiporal testes uniting before joining the duct from the poral testes. No irregularities were observed in these ducts although a number of proglottids were examined. It is not improbable, however, that such occur since they are so common in other species.

The cirrus sac (Fig. 76) contains a large internal seminal vesicle occupying about one-half of its interior when filled with spermatozoa. The cirrus is a narrow structure extending from the outer end of the latter to the opening into the genital cloaca through a mass of cells and muscles. It is somewhat coiled when not extruded. The pore is located on the anterior portion of the margin of the proglottid, and opens into a rather deep narrow genital cloaca with which the cirrus (above) and the vagina (below) communicate. The genital ducts both pass dorsal to the excretory ducts and the pore is always on the right hand side of the proglottid. The external seminal vesicle begins laterally just inside the excretory ducts and reaches to the center of the proglottid. It is an elongated cylindrical sac of about the same diameter when filled with spermatozoa. It is joined to the internal seminal vesicle by a somewhat coiled duct, which in ripe proglottids, becomes expanded in portions into reservoirs for spermatozoa.

In the female reproductive system the organs are also placed similarly to *W. macrostrobilodes*. The ovary is centrally placed between the poral and antiporal testes, and becomes large in ripe proglottids extending about half way across the testes on either side. It is slightly lobed in front, and somewhat curved anteriorly in the center. The vitelline gland is but slightly lobed and lies directly behind the central portion of the ovary.

The vagina is a thin-walled duct which opens into the genital cloaca ventral to the cirrus and usually lies ventral to the cirrus sac and external seminal vesicle. The portion medial to the excretory ducts becomes distended by spermatozoa in ripe proglottids, forming a seminal receptacle anterior to the poral testes and ventral to the external seminal vesicle. The uterus has the course indicated in figure 69 and described for *W. macrostrobilodes*. No mature eggs were observed in any specimens. The musculature does not show any marked differences from that as described for and figured for *W. macrostrobilodes*.

When the literature is examined with reference to the position of the testes, the following species are to be considered: *Weinlandia coronula* Dujardin 1845 has the three testes arranged in a similar manner, but they are much smaller in size, the proglottids are much shorter in proportion to the width of the worm than in the above described form, and the testes

are oval along the transverse axis of the proglottid. The musculature of *W. coronula* is very characteristic, the two longitudinal layers being very sharply differentiated while in both *W. macrostrobilodes* and *W. introversa* there is very little difference in size and location. The hooks are about the same size, shape, and number as in both *W. macrostrobilodes* and *W. introversa*, but in view of the above points one would have little difficulty in distinguishing the one from the other. *Weinlandia querquedula* Fuhrmann 1913 has a somewhat similar arrangement of the testes as both the latter named, but they are evenly rounded, not lobed, and the antiporal and poral are widely separated from each other, the space in between being occupied by the larger ovary, which extends the full length of the proglottid. The hooks are somewhat similar in shape, the anterior basal portion being somewhat less distinct, however, and the size  $14\mu$ , and the number 16.

Of the species which are found in Anseriformes, there are none which compare with these in length and number of hooks except those mentioned above. Of those concerning which nothing is known regarding the hooks, *W. lobata* Fuhrmann (1906: 352) has a similar arrangement of testes, but widely separated on the two sides of the proglottid and the space between occupied by the ovary. *H. megalhystera* v. Linstow (1905: 5) has hooks somewhat similar in shape, size, and number, but the testes are arranged in a transverse row.

### WEINLANDIA MICROCIROSOSA N. SP.

[Figs. 91-97]

The specimens of this species were obtained from the anterior one-fourth of the intestine of *Planesticus migratorius* (Linnaeus), the robin, killed at Urbana, Illinois, April 4, 1923. They were obtained from three hosts and are preserved in the author's collection under the numbers 112b2, 114b4, and 115b2.

The specimens are 30 to 36 mm long in a very much contracted condition. They were found to be most difficult to kill in anything like an extended condition. When allowed to remain in normal salt solution undisturbed, they would relax themselves to two or three times the above length, but when placed in the killing solution, they would immediately contract although attempts to keep them extended by stretching with the fingers or by shaking were made. When held extended in the fingers, they very readily pulled themselves in two in their efforts to contract. The only method tried that was even partially successful was to allow the worm to extend itself on a glass slide, and to quickly place another slide over it binding the two together with rubber bands, in which condition they were placed in the killing fluid. This resulted in specimens that were much contracted and in some instances poor fixation of the internal structures. Specimens killed in this manner were about 2 mm wide at their widest point

and 30 to 36 mm long. In life they are capable of extending to two or three times this length.

The scolex of the specimen from which the drawing was made is 0.1 mm wide, and has the four suckers directed forward in the contracted state. There is no neck region, since strobilization can be made out along the border at the widest portion of the chain opposite the rostellar sac. Behind this point, the strobila rapidly narrows to about one-half the above width and then gradually widens again. In one specimen, the scolex is but little wider than the anterior portion of the strobila. The rostellum is retracted into the rostellar sac in all the specimens studied, and is about 0.2 mm in diameter, evenly rounded and bears a single crown of ten hooks which are shaped like figure 93, and are about  $12\mu$  long.

In the male reproductive system the three testes are placed two in the posterior portion, one on either side of the ovary and the other in front of the antiporal posterior testes. The latter may be medial to, directly in front of, or lateral to the posterior antiporal testis. They vary much in size, but in specimens fixed in the partially contracted condition, they are about 200 by  $85\mu$ , being longest in the transverse axis of the strobila. Their ducts arise on the median border in each case. Occasionally there are two from a testis, but usually only one, and pass in an almost straight course to their point of union. The manner of union is variable as indicated by the drawings of four consecutive proglottids in figure 1. The vas deferens is short and connects with the external seminal vesicle which lies in front of the ovary in the right half of the proglottid. The external seminal vesicle is connected with the internal seminal vesicle by means of a duct which is gradually tapering laterally. The cirrus sac (Fig. 96) extends somewhat beyond the excretory ducts, and the larger part of its interior is occupied by the internal seminal vesicle. The walls of the vesicle and sac are rather heavy, and wide circular ridges along their sides are seen in cross section. These are more prominent in the outer half than the inner. The cirrus is short, straight, and spineless, and opens just dorsal to the vagina into the shallow genital cloaca. The pore is situated about one-fourth of the way back on the right hand margin of the proglottid.

In the female reproductive system the ovary is a deeply lobed transversely elongated organ located in the center of the proglottid. The vitelline gland lies just behind it and the vagina comes in from the right and anteriorly at about the middle of the proglottid. The seminal receptacle lies ventral to the external seminal vesicle, its inner end sometimes bending posteriorly around the paroral testes. It communicates with the genital cloaca through a long, slender, straight vagina which lies directly ventral to the cirrus sac and opens almost directly ventral to the cirrus.

The eggs in the uterus have three shells with the six-hooked embryos within. The two outer shells are very thin and often much distorted by

shrinkage. The average length of the outer is  $45\mu$  and width  $40\mu$ , with a maximum of 54 by  $45\mu$ , and a minimum of 42 by  $31\mu$ . The middle shell averages  $40\mu$  in length and  $31\mu$  in width with a maximum length of  $42\mu$  and a width of  $39\mu$ , and a minimum length and width of  $33\mu$  and  $23\mu$ . The embryo averages 38 by  $25\mu$  and has a maximum of 35 by  $38\mu$ , and a minimum length and width of 31 by  $21\mu$ . The hooks are 17 to  $20\mu$  long.

The longitudinal muscle layers are well developed, especially the outer one. The inner contains a much less number of bundles. The oblique muscles are very poorly developed, and in most proglottids none were found except in the outer angles. The regions separating the proglottids are clearly defined.

The large ducts of the excretory system are about 0.15 mm in diameter and the small dorsal duct about 0.05 mm in diameter, 1 cm from the scolex. No transverse vessels joining either of the longitudinal vessels could be traced.

The longitudinal nerve lies about 0.15 mm from the margin of the proglottid and under a point about one-fourth the length of the cirrus sac from its outer end.

When the descriptions of the various species are compared with the above description with reference to the position of the testes, the following deserve mention: *Weinlandia lobata* Fuhrmann (1906: 352) has the testes arranged in a similar position, and the cirrus sac is much like the one described above, but the onchosphere is  $16\mu$  in diameter, while in our species it averages 25 by  $38\mu$ . The scolex was absent from Fuhrmann's specimens but the length of the strobila is 14 cm, while the above described specimens were not over 8 cm long when fully extended, and but about 35 mm when fixed. *H. minor* (Krabbe) 1869 has hooks similar in shape and length but 14 in number. It is 25 mm long, and was found in *Phalaropus hyperboreus* (Linn.) a bird belonging to the Charadriiformes, while the robin belongs to the Passeriformes. *H. minor* is so poorly described that it ought to be disregarded as a species unless the original material can be restudied.

When compared with the species of *Hymenolepis* that have been recorded from the Passeriformes, there are only three which have similar hooks. *H. bilharzii* Krabbe 1869 has hooks that are much more strongly constructed in all parts and  $16\mu$  long. It is so poorly described that it must probably be disregarded. *H. palygramma* (von Linstow) 1875 has hooks  $17\mu$  long and was described from immature material having no sex organs. *Weinlandia importata* Fuhrmann 1918 has hooks 12 to  $16\mu$  long, but they are very slender and have a very long anterior basal portion and almost no posterior basal portion. There seems little doubt, therefore, that the above described species is new.

## WEINLANDIA PLANESTICI N. SP.

[Figs. 98-103]

The cestodes used in the study of this species were obtained from 9 specimens of *Planesticus migratorius*, robin, killed at Urbana, Illinois, between April 1 and May 1, 1923. They were taken from the middle three-fourths of the intestine and were found either attached to or free from the intestinal wall. The specimens are preserved in the author's collection under the numbers, 104, 105, 106, 108, 113, 114b, 123b, 125, 174b. Of this species cotypes were placed in the Ward Helminthological Collection at the University of Illinois, Urbana, nine mounts, comprising five totos and four sets of serial sections.

The specimens vary in length from 10 mm to 35 mm, and in width from 0.5 to 1.5 mm, depending on the stage of contraction and maturity of the worm. One specimen with mature eggs measured 20 mm long and 1 mm wide near the posterior end.

The scolex in all the specimens was strongly contracted and was about 0.2 mm broad, depending on the size of the worm. The suckers are strongly contracted, and are not raised appreciably above the surface of the scolex, the opening being directed forward. The rostellum is a strong muscular structure which is retracted into the rostellar sac as a solid muscular organ, and not as an introvert, the blades of the hooks always being directed backward. The rostellum carries a crown of ten hooks which have the shape represented in figure 101 and a length of about  $14\mu$ . Strobilization is evident immediately behind the scolex.

In the male reproductive system two of the three testes are placed on the posterior side of the proglottid, one poral and the other antiporal, and the third in front of the antiporal one. The latter is usually directly in front of the posterior testes, but in some specimens especially, its position varies, being placed either somewhat medially or laterally. The vasa efferentia are very variable in this form, as is indicated by the various figures. The number arising from each testes varies from 1 to 3, any testes may have any number up to three. Neither do the ducts pass directly to their point of union but may curve about and be joined by short ducts with each other giving the appearance of a network. Invariably, however, the ducts from the two posterior testes join before meeting those from the anterior testes. The testes are 0.06 to 0.08 mm in diameter in the region where the ovary and other female organs are well developed.

The vas deferens is a comparatively short duct. The external seminal vesicle communicates with the internal seminal vesicle through a short, usually somewhat coiled, duct. The internal vesicle is a simple sac, its inner portion being considerably larger than the outer and occupying about three-fourths the length of the cirrus sac. The cirrus is a slender tube and

is but slightly coiled, opening into the genital atrium dorsal to the opening of the vagina. Both the vagina and cirrus sac pass dorsal to the excretory vessels and the nerve, the large end of the cirrus sac lying directly above them. The pore is to be found slightly in front of the center of the proglottid, exactly on the margin, and on the right hand side.

In the female system the ovary lies in front of the two posterior testes and somewhat ventral to them. It is an elongate structure with irregular fan-shaped lobes on the anterior border. The vitelline gland lies behind it and is a rounded or oval organ without lobes. The seminal receptacle lies ventral to or somewhat posterior to the external seminal vesicle, and is very variable in shape, but generally elongated or oval in outline. The vagina is a long, wide, straight duct extending from the outer end of the seminal vesicle to its opening ventral to the opening of the cirrus in the genital atrium.

The eggs are very irregular in shape, due to shrinkage of the outer shells. The shells are very thin and the two outer have the space between them filled with material which is probably a loose cellular mass in the process of disintegration, while the space between the middle and inner shells is clear. The average size of the outer shell is 47 by 35 $\mu$ , with a maximum length of 56 $\mu$ , and a maximum width of 42 $\mu$ . It has a minimum length of 42 $\mu$  and a minimum width of 28 $\mu$ . The average length of the inner shell is 38 $\mu$  and the average width 27 $\mu$ , its maximum length and width being 44 and 33 $\mu$  respectively and its minimum 33 and 23 $\mu$ . The embryo has an average size of 32 by 24 $\mu$ , a maximum length and width of 40 and 30 $\mu$ , and a minimum length and width of 28 and 19 $\mu$ .

The inner longitudinal muscle layer contains about 25 bundles on each side of the proglottid, while the outer layer contains about 50 bundles.

The dorsal excretory vessel is somewhat smaller than the ventral, being about 18 $\mu$  in diameter, while the other is about 23 to 25 $\mu$  in diameter. Transverse vessels joining the longitudinal vessels have not been found.

A comparison of the above species with others necessitates a discussion of the following: *W. farciminosa* (Goeze) 1782, has hooks similar in shape, but 20 to 23 $\mu$  long, while in the above they are 14 $\mu$  long. Rosseter's (1908: 295) discussion of this species shows that the material which has been referred to it is in need of restudy since but little attention has been given the internal organs by most of the investigators, and Rosseter gives figures of the hooks from four sources which vary in shape. It is not possible to determine whether the material which Rosseter examined was identical with that of all the others or not on account of the incompleteness of the other descriptions. Fuhrmann (1908, footnote 4, p. 79) gives a discussion of its synonymy.

Of the species which have been described from Passeriformes whose size of hooks are near that of the above described form, the following should

be mentioned: *H. petrocinclae* Krabbe 1882 has hooks  $18\mu$  long, but very different in shape; *H. polygramma* (von Linstow) 1875, length  $17\mu$ , but the two lateral testes are lateral to the longitudinal excretory vessels according to Fuhrmann (1906: 734). *H. bilharzii* (Krabbe) 1869 has the blade shorter than the base, and the anterior portion of the base shorter than in the above described form; *Weinlandia serpentula* (Schrank) 1788, has hooks 24 to  $27\mu$  long, almost twice as long as in the form under discussion and a much longer and heavier anterior basal portion. Ransom (1909: 96) records this form from *Planesticus migratorus* with a question mark, but the reference which formed the basis for this statement is not given and has not been located during the present study. Fuhrmann 1908 does not include the name of the host in his list of cestodes under their hosts. It seems clear, then, that the form just described should be designated as a new species.



## GENUS WARDIUM NOV. GEN.

Diagnosis: Three testes in a proglottid. Position of the testes in the different proglottids of the strobila variable. Scolex armed with a single crown of hooks. Genital pores unilateral. Uterus sac-like. Genital ducts dorsal to the excretory canals.

Type species: *Wardium fryei* n. sp.

## WARDIUM CAPRIMULGORUM (FUHRMANN) 1906

Fuhrmann 1906c: 441 (Figs. 16-19); 1906e: 740.

Syn.: *Drepanidotaenia caprimulgorum* Fuhrmann 1906c,

*Hymenolepis caprimulgorum* Fuhrmann 1906e.

Hosts: *Nyctiprogne rupestris* (Spix), *Podager nacunda* Cab.

*Caprimulgus lineatus*.

Locality: South America.

Through the courtesy of Dr. Anton Collin, Director of the Zoologisches Museum der Universität, Berlin, Professor Ward received alcoholic material representing this species which was sent on loan and proved very valuable. For this courtesy the author desires to acknowledge here his indebtedness to the Museum and its Director.

Length 12 cm, width 1.5 mm. Testes variable in position. Cirrus sac small, not reaching the longitudinal excretory ducts. An internal and an external seminal vesicle present. Fuhrmann did not have any scolices when he first described the species, but he afterward found some and gives their description in 1906e: 740. They are 0.14 mm in diameter, and the rostellum is armed with 10 hooks which are 14 $\mu$  in length.

## WARDIUM CAPILLAROIDES (FUHRMANN) 1906

Synonym: *Hymenolepis capillaroides* Fuhrmann 1906.

Fuhrmann 1906b: 355.

Hosts: *Podiceps dominicus* (L.).

Locality: Brazil.

Alcoholic material representing this species was sent from the Zoologisches Museum der Universität, Berlin, through the Director, Dr. Anton Collin, to the Ward Helminthological Collection at the University of Illinois, Urbana, and was placed at the disposal of the author who is greatly indebted for these courtesies.

Length 3 cm, width 0.4 mm. Scolex 0.1 mm in diameter. Hooks are 10 in number and 21 $\mu$  long. Cirrus sac reaches beyond the longitudinal

excretory vessels but not beyond the center of the proglottid. The testes are arranged so that all three may lie in a transverse row or the antiporal testes somewhat anterior to or in front of the median testis. Ovary and vitelline gland median and small in size. Uterus sac-like and fills the entire interior of the proglottid.

Southwell (1916: 10) found several specimens of a cestode in *Corvus macrorhynchos*, a crow, at Calcutta, which he thinks possibly are *Wardium capillaroides*. This material should be restudied since the testes were observed to be regular in position, the posterior proglottids were square, and the details concerning the hooks could not be determined with certainty. The wide difference in the hosts is further indicative of different species.

### WARDIUM AMBIGUUM (CLERC) 1906

Synonym: *Hymenolepis ambiguus* Clerc 1906.

Clerc 1906a: 535.

Host: *Otis tetrax*.

Length 120 mm, maximum width 0.7 mm. Scolex 0.22 mm in diameter. Hooks 10 in number  $30\mu$  in length. Genital pores unilateral, and the genital ducts pass above the excretory vessels. Cirrus sac 0.18 mm long. External and internal seminal vesicle present. The only statement relating to the position of the testes is that they are variable according to the state of contraction of the strobila. There is, therefore, some uncertainty as to the exact genus to which this species should be placed. It should be restudied in order to determine its exact relationships.

### WARDIUM VARIABLE N. SP.

[Fig. 17-23]

Two specimens of this species were taken from the intestine of a specimen of *Corvus brachyrhynchos*, the common crow, killed at Monticello, Illinois, on November 10, 1923, and are preserved in the author's collection under the numbers 530.1 and 530.2. The length of one is 30 mm and its greatest width is about 1 mm near the posterior end. The other specimen is 20 mm long and 0.7 mm wide at its widest point. They each contain about 250 proglottids, of which the anterior 100 or so are very short in proportion to their width. Behind this point the reproductive organs rapidly develop, the testes first and the female farther back.

The scolex is conspicuous, being much wider than the anterior end of the strobila. It is about 0.2 mm wide or slightly less, while the width of the neck region is 0.06 mm. The suckers are 0.08 mm in diameter, and somewhat raised above the surface of the scolex. The rostellum was retracted in both specimens, in which condition it is a rounded organ about

0.02 mm in diameter. It is armed with a single crown of hooks which measure from 20 to 22 $\mu$  in length. The base is much curved and for this reason the shape of the hook may be easily misjudged unless one is careful to observe one which lies with all its parts as nearly as possible in the same plane of focus.

The testes are regularly three in number, although four proglottids were found out of 102 which had four each and one had but two. Their arrangement in 67 of the 102 cases was two on the posterior border and one antiporal and lateral to the posterior antiporal testes. Four had the anterior antiporal testis in front and one medial to the posterior antiporal testis, while eleven proglottids had the three organs in a row on the posterior border. In nine instances the two lateral testes were both anterior to the median which was on the posterior border of the proglottid; in five proglottids two were poral, one testis being anterior and lateral to the posterior, and but one instance was found where two only were observed, they being on the antiporal side.

The cirrus sac extends medially about one-third the width of the proglottid and in each instance observed contained a relatively small internal seminal vesicle. However, the latter was not observed distended with spermatozoa. It is thick walled and has a layer of small nuclei about its outer margin. The cirrus extends from the outer end of the internal seminal vesicle outward and extends through about two-thirds of the length of the sac. It opens into the genital cloaca dorsal or anterior to the vagina. The genital cloaca is a wide rounded cavity up into which an elevation of the surrounding tissue of the proglottid extends. The pore is to be found about one-fourth the way back on the right hand margin of the proglottid. The external seminal vesicle lies directly in front of the vitelline gland and ovary, the latter extending beneath it when reaching maturity.

The ovary lies in the anterior ventral portion of the proglottid, beneath the external seminal vesicle and the vagina. It is divided by deep constrictions on the anterior side into several lobes up to about six in number which extend anteriorly and laterally in a fingerlike manner. The whole organ is somewhat bent anteriorly in the center, and has the vitelline gland and shell gland placed in the posterior concavity. When fully developed, it extends somewhat farther laterally than shown in figure 22a, but never reaches to the excretory vessels. The vagina lies beneath or slightly posterior to the cirrus sac and is a rather thick-walled duct which widens out at its inner end to form a seminal receptacle dorsal to and behind the ovary. The vitelline gland is a spherical or oval organ lying just behind the ovary. Between the ovary and vitelline gland or slightly more ventral, the shell gland is to be found. The uterus is a transverse sac which is irregularly divided by partial septa into several lobes. The eggs were present in large numbers, but in neither of the specimens obtained were they

mature. A few large single cells were observed which apparently were unfertilized eggs and consequently had not developed.

The ventral longitudinal ducts are considerably larger than the dorsal, as is usual in this group of cestodes, being about 35 by 25 $\mu$  in diameter, while the dorsal are 14 $\mu$  in diameter. The large ventral vessels are connected by transverse vessels 7 $\mu$  or wider in diameter, while no such connections occur between the dorsal vessels. Occasionally these transverse vessels are branched at the end (Fig. 23). The longitudinal nerve lies on each side usually about half way between the excretory vessels and the border of the proglottids. The longitudinal muscles are differentiated into two well defined and widely separated layers (Fig. 17). The inner one contains about a dozen bundles on a side. The outer contains about 20 to 25 bundles which are about 5 $\mu$  in diameter while the inner are about 12 $\mu$  in diameter.

A discussion of this species with reference to the literature is indeed difficult when considered with reference to the position of the testes. One of the most satisfactory descriptions of a species with testes variable in position is that of *W. caprimulgorum* Fuhrmann (1906c: 441), collected in Brazil from *Nactiprogne rupestris*, *Podager nacunda* and *Caprimulgus lineatus*. The most outstanding differences are, however, the very small cirrus in *W. caprimulgorum*, where it reaches only about half way to the excretory vessels on the poral side, and the hooks which are 14 $\mu$  long, while in the above described form they are about one-third longer, the anterior portion of the base being much shorter than in that described above. The difference in the orders of birds to which the hosts belong is also marked, that of *W. caprimulgorum* being Coraciiformes while the crow to the Passeriformes. Another species which is recorded as having testes variable in position is that of *W. capillaroides* Fuhrmann 1906, but in this the testes are smaller and the two on the antiporal side are some distance removed from the poral testes, the pore is in the center of the proglottid, while in the above described form it is only one-third the way back on the border. The hooks, although of about the same size, are more slender in structure throughout while the host of *W. capillaroides* is a grebe.

When the literature is examined with reference to the species that have been recorded from the Passeriformes, it is found that there are, in all, 24 species. When the size of the hooks from these various species are compared, it is found that only those species included in the following comparative table agree near enough in size to be considered. In the following table some of the important characters are compared with the species described above.

From the following table one sees that the hooks of *W. variabile* differ in shape from those of the other species infecting Passeriformes which have hooks of a similar length. Four of the species have the location of the testes very inadequately described and no statement is made as to the

TABLE I

Comparison of Somewhat Similar Species			
	Position of testes	Shape of hooks	Size of hooks
<i>Wardium variable</i>	67% Variable	Blade and 2 parts of base about equal	20 to 22 $\mu$
<i>H. hemignathi</i>	Transverse row	Blade very long	18 to 23 $\mu$
<i>H. petrocinctae</i>	?	Anterior portion base very long	18 $\mu$
<i>W. passerina</i>	2 antiporal 1 before the other	Ant. portion base very long, blade and post. portion base very short	20 $\mu$
<i>W. interruptum</i>	2 antiporal 1 before the other	Ant. portion of base much longer than post and blade	20 $\mu$
<i>W. microscolecina</i>	2 antiporal 1 in front of other	Blade and 2 parts of base about equal but ant. portion of base much heavier than in above described form	23 $\mu$
<i>W. farciminosum</i>	Straight line?	Both parts of base much heavier than in above described form	21 $\mu$
<i>W. serpentulum</i>	2 poral, 1 before other, separated from other posterior	Post. part of base very heavy	25 to 27 $\mu$
<i>W. globocephalum</i>	2 antiporal, 1 in front of other, but small and separated far from poral testes	Very heavy in structure in all parts	19 $\mu$

variability of their position in any of the descriptions. No records are given by Fuhrmann (1908) of any cestodes from any of the species of crow in North America. It seems quite clear then that this species is new.

#### WARDIUM FRYEI N. SP.

[Figs. 24-31]

The material from which this description was written was obtained from the intestine of a specimen of *Larus glaucences*, the glaucous-winged gull, killed in San Juan county, Washington, July 20, 1923, and is preserved in the collection of the writer under the number 276.

The specimens are very slender cestodes which measure 115 mm in maximum length but do not exceed 1 mm in width at their widest point. The anterior 25 to 30 mm is very slender, and disintegrates very early after the death of the host. The male sex organs are well developed in

proglottids 20 to 30 mm from the scolex, and the beginning of the female organs is well differentiated. It should be noticed especially at this point that the start of the ovary in the early stages and the fully formed organ may be very easily confused with the testes and therefore it is only possible to identify these organs with certainty from sections. Frontal sections are the most useful as the ovary is ventral and is not obtained to any great extent in sections containing the testes. Because of the great variability of the position of the testes, these organs cannot be identified by their location as they can in species characterized by regularity of position. Proglottids about 50 mm from the scolex are about 0.35 mm in transverse diameter by 0.2 mm in thickness, while at the extreme posterior end they are usually less than 0.8 mm wide. The pore is unilateral and on the right hand side of the proglottid.

The scolex is somewhat larger than the strobila immediately behind, it being about  $106\mu$  while the strobila is about  $70\mu$  in width. The rostellum is short, rounded, and armed with a single crown of ten hooks. But three scolices were obtained, from two of which the hooks had been lost. The other had ten hooks, 17 to  $19\mu$  long, shaped like figure 26. The rostellum was not retracted, although there was a deep rostellar sac extending as far back into the scolex as the posterior border of the suckers. In so far as it could be made out, the rostellum seemed to be retracted as a solid organ and not as an introvert.

The three testes are placed in an irregular manner, the proglottids in which they are placed in an almost transverse row are somewhat more numerous than are those with the other arrangements. They may, however, be placed so that two are on the posterior side and the other directly in front or somewhat lateral to either the poral or antiporal testis, or one may be median and posterior and the others one on either side and somewhat anterior to it. Of 169 proglottids examined, of which about an equal number were counted for each of four specimens, the testes were distributed as follows: 45 had all three in a row; 55, one was posterior and one on each side and anterior to it; 50, two posterior and the other anterior or lateral to antiporal testes, and 19 in which two were posterior and the other anterior or lateral to the poral testes. The testes are crowded ventrally or dorsally, or indented by the cirrus sac and external seminal vesicle, depending upon the stage of development of the organs, the ripe proglottids being very well filled in the central portion by reproductive organs.

The cirrus sac is very large and occupies the anterior half of the poral side of the proglottid, opening into the genital cloaca which lies on the right hand side of the proglottid a little in front of the center of the border of the proglottid. It appears very early and soon comes to contain the very large cavity of the internal seminal vesicle, which occupies the larger part of the interior, and almost fills it when filled with spermatozoa. The cirrus

is a thick fleshy organ, the duct of which is thin walled and much coiled in the unextruded organ. It opens into the internal seminal vesicle at the outer end of the latter. What appears to be the cirrus when extruded is seen to contain numerous small nuclei and to be made up of loose connected tissue, the outer surface being entirely free from hooks or spines (Fig. 10). The external seminal vesicle is a large thin-walled sac which lies just medial to the inner end of the cirrus sac and communicates with it through a short, wide, somewhat coiled duct. The external seminal vesicle and cirrus sac together reach a little more than half way across the proglottid in most cases.

The ovary (Fig. 28) is an irregularly lobed organ lying posteriorly in the proglottid and ventral to the testes, the anterior portion of the proglottid being occupied by the cirrus sac and external seminal vesicle. The vagina lies directly ventral to the cirrus sac and opens into the genital cloaca ventral to the cirrus (Fig. 22). It is a clearly defined, heavy-walled duct somewhat coiled and widens out forming the seminal receptacle which lies just ventral to the inner end of the cirrus sac. The vitelline gland is irregularly rounded or oblong, and lies dorsal and anterior to the ovary and ventral to the testes and cirrus sac.

The uterus is a transverse sac divided incompletely into compartments by septa and well filled with eggs in the mature proglottids. The embryos are oval in shape and average  $34$  by  $28\mu$  in size but range from  $28$  to  $40\mu$  long by  $23$  to  $40\mu$  wide. Figure 25 represents about an average shape but they are often more elongate or more rounded. The outer shell ranges in diameter from  $37$  to  $52\mu$  by  $26$  to  $49\mu$  and averages  $26$  by  $37\mu$ . The inner shell is closely applied to the embryo, but two shells could be made out on any of the eggs. Although the hooks are well developed and apparently fully formed, no trace of the middle shell could be found. Ransom found a somewhat similar condition in the eggs of *Hymenolepis cantianiana*, differing however, in that the contents of the egg of the latter is separated into two regions separated by a very thin membrane. The hooks are often found extending through the outer shell, and are very prominent, having a characteristic enlargement on the shaft about three-fourths the distance from the inner end. This enlargement in many appears to go entirely around the shaft while in others this is not apparent. The hooks are from  $14$  to  $17.5\mu$  in length, and great care must be used in selecting those to be measured in order to have the entire hook as nearly in the same plane of focus as possible.

It is difficult to make a comparative study from the literature of the forms known to show variability in the position of the testes. Earlier workers apparently failed to appreciate the possible importance of recording such variations in an exact manner. Fuhrmann seems to be almost the only investigator who has taken any notice of this fact, and has described two

species as having this peculiarity. These are *W. caprimulgorum* Fuhrmann 1906 and *W. capillaroides*. Aside from the great difference in the hosts, the hooks are very different in shape, in that they both have well-developed anterior basal portions, while the above described species has none at all. *W. ambiguum* Clerc 1906 has testes somewhat variable in position but the hooks are almost twice as long, and it has a long anterior basal portion. *H. clandestina* (Krabbe) 1869 is the fourth species to which reference has been made to the testes being in a variable position, but here again the hooks have a long anterior basal portion and are twice as long as in the case of the above described form.

Five species of *Hymenolepis* have been recorded from the Lariformes. All five of them have hooks very different in shape, or of a different number, from those in the species first described, as well as other characters. It seems proper to conclude that the above described species should be designated as new.



## GENUS ECHINORHYNCHOTAENIA FUHRMANN 1909

Generic diagnosis: Genital pores unilateral. Genital ducts pass between the longitudinal excretory vessels. Testes three in number. Uterus sac-like. Rostellum proboscis-like and covered with hooks.

Type species: *Echinorhynchotaenia tritesticulata* Fuhrmann 1909.

This genus was erected by Fuhrmann to accommodate *E. tritesticulata* and placed in the family Dilepinidae. The number of the testes in the two species thus far assigned to it, however, is believed to justify its transfer to the family Hymenolepididae. The internal anatomy is indeed similar to that found in the genera *Wardium* and *Hymenolepis*, but in view of the constancy of the position of the genital ducts with reference to the excretory ducts in the species studied and the probable systematic importance of this character, the retention of the genus *Echinorhynchotaenia* seems justified at the present time. Although the structure of the proboscis has not been studied, it is probably not much different from an introvert. The main difference between the introvert and the rostellum retracted as a solid body is in the degree of muscular development and arrangement, and serves as an important specific character but is not of generic value. The arrangement of the hooks is, likewise, of less importance than the internal structures of the proglottids.

## ECHINORHYNCHOTAENIA TRITESTICULATA FUHRMANN 1909

See Fuhrmann 1909:32-35, (Figs. 28-31)

Host: *Ankinga rufa* (Lacep. Dand)

Locality: Africa

Length 30 cm, width 4 to 5 mm. Testes variable in position and 3 in number. Genital pores unilateral. Genital ducts pass between the longitudinal excretory vessels. Ovary divided into two portions, each deeply lobed. Uterus sac-like and lobed.

ECHINORHYNCHOTAENIA NANA MAPLESTONE  
AND SOUTHWELL 1922

See Mapleston and Southwell 1922:193-197, (Figs. 5-7)

Host: *Chenopsis atrata*, Lath., the black swan.

Locality: Townsville, North Queensland.

Length 2 cm, width 1.7 mm. Scolex 1.5 mm wide and 2.3 mm long. Behind each sucker is a lappet. Segments broader than long. Genital pores unilateral, and open on the right hand side of the proglottid. Longi-

tudinal muscles in two layers. Unfortunately the proboscis had apparently been torn out, but the "appearance of the head, with a few ragged fibers protruding from the central pit, leaves no room for doubt that a proboscis has been present." The material was in a bad state of preservation and could not be completely described in other respects. The relation of the genital ducts to the excretory vessels was not stated. This species should be more completely studied from material in a better state of preservation with the view of determining more accurately its relationships.

#### GENUS HYMENOFIMBRIA SKRJABIN 1914

Generic diagnosis: Three testis in a proglottid. Scolex with a single crown of hooks. Genital pores unilateral. Excretory system consisting of ten longitudinal vessels. Uterus a simple sac. Longitudinal musculature consists of a single layer. Strobila well marked off into proglottids. Pseudo-scolex absent.

Type species: *Hymenofimbria merganser* Skrjabin 1914.

#### HYMENOIMBRIA MERGANSERI SKRJABIN 1914

See Skrjabin 1914:473-476.

Host: *Mergus merganser*

Locality: Russian Turkestan

The exact length of the parasites could not be given since the type material consisted of fragments, but they were estimated as being about 120 to 150 mm. The maximum width has 4 mm. The scolex is 0.14 mm long by 0.17 mm wide. The rostellum is armed with 10 hooks which are 18 $\mu$  long and are shaped like *Haploparaxis filum*. The neck is 0.148 mm wide and 0.3 mm long.

The musculature consists of a transverse layer and a single row of longitudinal bundles. The longitudinal bundles measure 34 to 41 $\mu$ , and each consists of from 40 to 50 fibers. There is also a diagonal muscular layer outside of the longitudinal. The excretory system consists of ten parallel longitudinal vessels. The lateral vessels are asymmetrically placed, two lying outside the longitudinal nerve on one side while on the opposite they are median to the nerve. The three testes lie in a transverse row, one being poral and the other two antiporal to the female reproductive glands. The female reproductive glands are median, and are relatively small. The ovary is somewhat indented on the anterior margin, while the vitelline gland is median and directly behind the ovary. The uterus is sac-like and extends the entire width of the proglottid.

#### GENUS FIMBRIARIA FROELICH 1802

Scolex small and usually lost, with rostellum armed with a single row of hooks. Strobila without true segments, but with transverse grooves

giving the appearance of segments. Pseudoscolex retains the true segmentation. Excretory system consists of several pairs (three and eleven in the two known species) of longitudinal excretory vessels. Genital pores marginal, unilateral, and on the right hand border of the strobila. Testes three in number for each cirrus pouch. Ovary, reticular or forming network extending through the strobila, or a single simple ovary for each set of reproductive organs. Uterus reticular for the species known.

Type species *Fimbriaria fasciolaris* (Pallas 1781).

#### FIMBRIARIA FASCIOLARIS (PALLAS) 1781

Synonyms, *Taenia fasciolaris* Pallas 1781; *T. malleus* Goeze 1882; *Fimbriaria malleus* Fröhlich 1802; *Fimbriaria mitra* Fröhlich 1802; *Alyselminthus malleus* (Goeze 1782) Zeder 1800; *Halysis malleus* (Goeze 1782) Zeder 1803; *T. trilineata* Batsch 1786; *Taenia pediformis* Krefft 1871; *Episium plicatus* Linton 1892; *Fimbriaria plana* von Linstow 1905; *Notobothrium arcticum* von Linstow 1905.

This species has been very much misunderstood and hence has resulted the long list of synonyms recorded above. Its anatomy is very well described by Wolffhügel 1900, but the true nature of the pseudoscolex, and the arrangement of the reproductive organs were not fully described. These points have been very clearly elucidated by Fuhrmann, 1914, who arrived at the conclusion that the pseudoscolex, instead of being an abnormal portion of the strobila is the most normal, and that there were three testes for each cirrus sac which are arranged in a linear series. For a description of this species, the reader should refer to Wolffhügel 1900, and to Fuhrmann 1914.

#### FIMBRIARIA INTERMEDIA FUHRMANN 1914

This species is well described by Fuhrmann (1914: 446) and was obtained from the digestive tract of *Somateria mollissima*. For a detailed description the reader is referred to his account.

## SUBFAMILY DIORCHINAE

Subfamily diagnosis: Hymenolepididae with regularly two testes in each proglottid.

Type genus: *Diorchis* Clerc 1903.

## GENUS DIORCHIS CLERC 1903

Two testes in a proglottid. Rostellum armed with a single crown of ten hooks in all the described species. Suckers unarmed or armed with minute spines. Inner longitudinal muscle layer consisting of eight bundles, four dorsal and four ventral. Genital pores unilateral. Uterus sac-like. In birds.

Type species: *Diorchis acuminata* (Clerc 1902) Clerc 1903.

## DIORCHIS ACUMINATA (CLERC) 1902

See Clerc 1903:281-284, (Figs. 25, 78, 88); Ransom 1909:42-48, (Figs. 30-36).

Hosts: *Nettion crecca*, *Mareca penelope*, *Chauleasmus streperus*, *Fulica atra*, *Fulica americana*.

Locality: Europe and North America.

This species is well described by Ransom and Clerc, and the following description is based upon the details given in their accounts. The hooks are ten in number and  $38\mu$  in length. The length is 35 mm and the width 0.65 mm. The full-grown worm is probably somewhat longer, as the final segments were not gravid in Ransom's material. The longitudinal muscles are typical of the genus and consist of two layers, the outer composed of numerous small, and the inner of eight large bundles. The excretory vessels lie so that the dorsal is directly above the ventral, and are not connected by transverse vessels. The cirrus sac and vagina pass dorsal to the excretory vessels and nerve. The two testes are located near the dorsal surface in the posterior portion of the segment, one on either side of the median line, and reach a maximum size of 100 to  $130\mu$ . An internal and an external seminal vesicle is present. Cirrus sac is elongated, extending transversely across the proglottid, its inner end not reaching the median line. The cirrus is unarmed and has a globular swelling at its base. The vagina forms a seminal vesicle median to the excretory ducts and reaches the inner end of the cirrus sac. The ovary is trilobed, one lobe being anterior and median and the others lateral, often by a division of the left lateral it becomes four-lobed. When fully developed, it extends laterally as far as the excretory canals and the median lobe extends forward to the anterior border of the segment. The yolk gland is spherical, 45 to  $60\mu$  in diameter,

located in the median line and behind the middle of the ovary. The uterus is sac-like, developing large lobes which penetrate between the longitudinal muscles and beyond the longitudinal excretory vessels. The eggs are elongate. Jacobi (1898) described the anatomy of *Taenia inflata* Rudolphi, a species very similar to *D. acuminata*, but Ransom thinks this should be regarded as a separate form.

### DIORCHIS AMERICANA RANSOM 1909

See Ransom 1909:48-51

Host: *Fulica americana*

Locality: Nebraska, United States.

The length of specimens of this specimens in which eggs were not yet fully mature was 20 to 25 mm and the maximum width 0.6 mm. Rostellum armed with ten hooks 65 $\mu$  long. Suckers covered with minute spines. The genital pores are unilateral on the right-hand margin of the strobila at about the middle of the proglottid. Nervous system and musculature similar to those in *D. acuminata*. Vagina and cirrus pouch dorsal to the nerve and excretory vessels.

The testes, two in number, of a maximum size of 100 to 130 $\mu$ , are located in the posterior portion of the segment, dorsal and one on either side of the median line. The cirrus sac extends beyond the median line. Internal and external seminal vesicles are present. The cirrus is very slender and without bulbous enlargement at the base.

The vagina forms an elongated seminal receptacle median to the excretory ducts which extends as far medially as the cirrus sac. The ovary is trilobed with occasionally a fourth lobe on the left hand side. Yolk gland similar in shape and location to these organs in *D. acuminata*. The uterus is a simple sac, and, when fully developed, extends from the posterior to the anterior border of the segment and laterally beyond and dorsal to the excretory canals on the right and ventral to the excretory canals on the left side of the proglottids. Eggs containing fully developed oncospheres were not present in the type material.

### DIORCHIS FLAVESCENS (KREFFT) 1871

See Kreff 1871:15 and Johnston 1912:15

Hosts: *Anas superciliosa*, *Spatula rhynchotis*, *Nettion castaneum* and *Aythya australis*.

Locality: Australia.

This species was originally described by Kreff 1871 under the name of *Taenia flavescens*. His description was very insufficient, but fortunately, the type material was reexamined and a very satisfactory description given by Johnston (1912).

The specimens were from 3 to 5 cm in length in most cases but some were as long as 8.4 cm. The suckers are armed with minute spines. Ros-

tellum armed with ten hooks  $68\mu$  long, arranged in a single circle. Longitudinal musculature arranged in two series, an outer of numerous small and an inner of eight large bundles. Genital ducts pass dorsal to the excretory vessels. Genital pores are unilateral on the right hand side of proglottid. The two testes are medially placed and attain a size of 0.1 mm. Cirrus sac reaches the middle line and sometimes much farther. An internal and an external seminal vesicle present. Ovary compact, trilobed, and medially placed on the ventral side of the proglottid. When mature the ovary reaches from the excretory vessels of one side to those of the other, one lobe being median and anterior while the others are lateral. The yolk gland is rounded or kidney-shaped and more dorsal in position than the ovary. Vagina forms a seminal receptacle. The uterus extends beyond the excretory ducts, lying dorsal to them on the poral side, but ventral on the antiporal side of the proglottid. Mature eggs are from 90 to  $107\mu$  in length and from 27 to  $31\mu$  in width. Each end is somewhat bluntly pointed, while each extremity of the inner shell is produced into a very prominent process. The inner shell measures from 54 to  $68\mu$  in length by about  $16\mu$  in breadth.

#### DIORCHIS INFLATA (RUDOLPHI) 1809

See Krabbe 1869:285-286, (Figs. 109-11) (*Taenia inflata*). Jacobi 1898:95-104, (pl. 6, 16 fig.) (*T. inflata*); Cohn 1901 :330-331, *Hymenolepis inflata*; Clerc 1903:284-288, (Fig. 89); von Linstow 1906:15-17, (Figs. 17-18), (*H. inflata*)

Host: *Fulica atra* (L.)

Locality: Europe.

The length of this cestode is 80 to 100 mm and its width is 2 to 3 mm. The ten hooks are  $23\mu$  long, according to Jacobi. The testes are large and centrally located in the proglottid, the two reaching to the excretory vessels on either side. The ovary and vitelline gland are centrally located. The cirrus sac does not reach the center of the proglottid. The above data are from Jacobi, and since the species has not been reported in the western hemisphere, further details are not included in this report.

#### DIORCHIS PARVICEPS (VON LINSTOW) 1872

See von Linstow 1872-57 (Figs. 11-12); 1904:306-307 (Figs. 23-25)

Host: *Mergus serrator*.

Locality: Europe.

The length of the specimens of this species is recorded as being 110 mm, and 2.16 mm in maximum width. The pores are unilateral and marginal. The rostellum has ten small hooks  $12\mu$  long. The two testes are oval, 130 by  $79\mu$  in size. Ovary consists of a number of parts arranged rosette-like in the center of the proglottid. The vitelline gland is located in the center of the ovarian group.

## DIORCHIS EXCENTRICUS N. SP.

A number of specimens of a small species of *Diorchis* were taken from the posterior half of the intestine of *Erismatura jamaicensis*, the ruddy duck, killed at Peoria, Illinois, November 23, 1923. They are preserved in the author's collection under the number 576b.

The length of these worms varies from 26 mm to 52 mm. Even the longest specimen contained no mature eggs, and the uterus was not yet developed in any of the posterior proglottids. The width of proglottids about 30 mm behind the scolex is about 0.7 mm and in the longest a maximum width of 1.4 mm near the posterior end of the strobila. Immediately behind the scolex, the proglottids are about 190 $\mu$  wide. The pores are unilateral and on the right hand side of the proglottid.

The scolex is relatively inconspicuous. It is scarcely wider than the strobila immediately behind, but the suckers extend outward on each side, marking off this region from that immediately behind. Its length and width are about equal, about 175 $\mu$ . The rostellum is about 75 $\mu$  long when extended, and has a slightly enlarged distal portion about 70 $\mu$  in diameter. It carries a crown of ten hooks, each of which is shaped as shown in figure 107. In length they measure 26 $\mu$  to 31 $\mu$ . When retracted the blades of the hooks are directed backward, showing that it is retracted as a solid muscular organ.

In the male reproductive system the two testes are large organs occupying the larger part of the interior of the proglottid. They are transversely placed in the posterior portion of the proglottid and somewhat toward the poral side, the ovary being slightly in the antiporal portion. The poral testis is regularly found almost directly dorsal to the longitudinal excretory ducts on that side. The nerve is found ventral to that portion of the testis. The antiporal testis reaches the excretory vessels of the antiporal side. There are two testes in each proglottid in each case observed and their position is very constant.

The cirrus sac is elongated and of about the same diameter throughout its entire length, and reaches somewhat beyond the excretory vessels on the poral side. A rounded external seminal vesicle is located at the inner end of the cirrus sac. The cirrus is large and thickly set with conspicuous spines. The internal seminal vesicle occupies the larger part of the cirrus sac. The genital ducts lie dorsal to the longitudinal excretory vessels and the pore is on the right hand side of the proglottid.

In the female reproductive system the first trace of the ovary is located on the ventral side and near the antiporal excretory vessels. As sexual development proceeds, the ovary grows laterally beneath the excretory ducts, and medially, reaching, when fully developed, to the poral excretory ducts or slightly beyond. When extending beyond the excretory vessels on the poral side, it lies dorsal to them, which is due to the ventral dis-

placement of the ducts by the cirrus sac and testis. The ovary at no time is conspicuously lobed, but in its earlier stages has a few shallow constrictions along its margin. The vitelline gland is a rounded, oval, or egg-shaped organ lying directly posterior to the ovary. The vagina is a thin-walled duct leading directly from the region of the vitelline gland to the pore. It is sometimes distended throughout almost its full length by spermatozoa, but usually only its inner end functions as a seminal receptacle.

The two layers of longitudinal muscles are well differentiated. The inner one is composed of eight large bundles, four ventral and four dorsal and placed as indicated in figure 106. The outer contains numerous much smaller bundles arranged in an almost symmetrical row in the outer portion of the proglottid.

Of the species of *Diorchis* which have been previously described, there are none which show much similarity either in shape of hooks or the arrangement of the internal organs. The two species which have been described from America have the testes median in position and hooks with a much longer blade in proportion to the base. The hooks of *D. americana* are about twice as long as in the above described species. In *D. acuminata*, whose hooks are about the same in length as those described above, the ovary is median, deeply lobed, and smaller, while in our species it is antiporal, transversely elongated, and scarcely lobed.



## SUBFAMILY HAPLOPARAXINAE

Subfamily diagnosis: Hymenolepididae with regularly a single testis in each proglottid.

Type genus: *Haploparaxis* Clerc 1903.

## GENUS HAPLOPARAXIS CLERC 1903

Number of testes, one. Scolex with rostellum armed with a single row of 10 to 46 hooks in the species described. Genital pores unilateral. Genital ducts pass above the excretory vessels in all the species so far mentioned except *H. furcigera* (Rud. 1819) Fuhrmann 1908, which has the genital ducts passing between the excretory vessels and ventral to the nerve, according to von Linstow (1905, figure 8, p. 23). Uterus a simple sac. In birds.

Type species: *Haploparaxis filum* (Goeze 1782) Clerc 1903.

## LIST OF SPECIES

*Haploparaxis australis* Johnston 1911. See Johnston 1911:90

Host: *Gallinago australis*

Locality: Australia

Hooks: 8, 19 to 22 $\mu$  in length

Eggs: 57 by 42 $\mu$ ; oncosphere 34 by 25 $\mu$

*Haploparaxis brachyphallos* (Krabbe 1869)

See Krabbe 1869:310-311 (*Taenia brachyphallos*)

Syn: *Hymenolepis brachyphallos* (Krabbe) Fuhrmann 1906

*Skorikowia clausa* von Linstow 1905

*Diorchis serpentata* von Linstow 1905

Hooks: 10, 17 to 18 $\mu$  in length

*Haploparaxis cirrosa* (Krabbe 1869) Clerc 1903

See Krabbe 1869:308 (*Taenia cirrosa*); Clerc 1903:269-271.

Hooks: 10, 24 $\mu$  in length

*Haploparaxis crassirostris* (Krabbe 1869) Clerc 1903.

See Krabbe 1869:314 (*Taenia crassirostris*); Clerc 1903:265-267.

*Haploparaxis diminuens* von Linstow 1905.

See von Linstow 1905b:8-9.

Hooks: 10, 14.3 $\mu$  in length.

*Haploparaxis dujardinii* (Krabbe 1869) Clerc 1903.

See Krabbe 1869:319-320 (*Taenia dujardinii*); Fuhrmann 1895:436 (*Taenia dujardinii*);

Clerc 1903:274-275.

Hooks: 46, 16 to 18 $\mu$  in length.

*Haploparaxis elisae* Skrjabin 1914.

See Skrjabin 1914:451.

Hooks 10, 25.9 $\mu$  in length.

- Haploparaxis filium* (Goeze 1782) Clerc 1903.  
See Krabbe 1869:312-313 (*Taenia filum*); Clerc 1903:257-263.  
Hooks: 10,  $17\mu$  to  $18.5\mu$ .
- Haploparaxis furcigera* (Rud. 1819) Fuhrmann 1908.  
See Krabbe 1869:315 (*Taenia rhomboidea*);  
Stiles 1896:34-35 (*Dicranotaenia furcigera*).  
Hooks: 10,  $47\mu$  to  $58\mu$  in length.
- Haploparaxis hirsuta* (Krabbe 1882) Clerc 1902, 1903.  
See Krabbe 1882:9 (*Taenia pubescens*); Clerc 1903:267-269.  
Syn: *Taenia pubescens* Krabbe 1882, *Monorchis hirsuta* Clerc 1902.  
Hooks: 10,  $37\mu$  to  $39\mu$  in length.
- Haploparaxis larina* Fuhrmann 1901.  
See Fuhrmann 1901-03:518-520.  
Hooks: 10,  $21.6\mu$  to  $23\mu$  in length.
- Haploparaxis murmanica* Baylis 1919.  
See Baylis 1903:512-513.  
Hooks: 10,  $65\mu$  in length.
- Haploparaxis penetrans* (Clerc 1902).  
See Clerc 1903:271-274.  
Hooks: 10,  $40\mu$  long.
- Haploparaxis sphaerophora* (Rud. 1810) Fuhrmann 1906.  
See Fuhrmann 1906e:739.
- Haploparaxis fuligulosa* Solowicw 1911.

## SPECIES INQUIRENDAE

- Hymenolepis bilharzii* Krabbe 1869. See Krabbe 1869:73
- Hymenolepis brevicirrosa* Fuhrmann 1918. See Fuhrmann 1918:402
- Hymenolepis cantianiana* (Polonio 1860) Ransom 1909. See Ransom 1909:36-41
- Hymenolepis dakurica* von Linstow 1903. See von Linstow 1903: 290.
- Hymenolepis exilis* (Dujardin 1845) Fuhrmann 1906. See Stiles 1896:58
- Hymenolepis fusa* Krabbe 1869. See Krabbe 1869:307
- Hymenolepis fringillarum* (Rudolphi 1809). See Krabbe 1869:326
- Hymenolepis filirostris* (Wedl. 1856). See Wedl. 1856:15
- Hymenolepis fallax* (Krabbe 1869). See Krabbe 1869:71
- Hymenolepis groenlandica* (Krabbe 1869). See Krabbe 1869:68
- Hymenolepis liophallos* (Krabbe 1869). See Krabbe 1869:43
- Hymenolepis minor* (Krabbe 1869) (*T. minuta*). See Krabbe 1869:292
- Hymenolepis macracanthos* von Linstow 1877. See Linstow 1877:16
- Hymenolepis micrancristota* Wedl 1856. See Wedl 1856:6
- Hymenolepis naja* (Dujardin 1845). See von Linstow 1872:57.
- Hymenolepis orientalis* (Krabbe 1879) Fuhrmann 1906. See Krabbe 1879:11, 1882:360
- Hymenolepis petrocinctae* (Krabbe 1882). See Krabbe 1882:356
- Hymenolepis parvirostellata* von Linstow 1901. See von Linstow 1901:426.
- Hymenolepis polygramma* (von Linstow 1875). See von Linstow 1875:186.
- Hymenolepis paculifera* (von Linstow 1879). See von Linstow 1879:186.
- Hymenolepis pigmentata* (von Linstow 1872). Fuhrmann 1906. See von Linstow 1872:56.
- Hymenolepis recurvirostrae* (Krabbe 1869). See Krabbe 1869:60
- Hymenolepis rosseleri* Blanchard 1891. See Blanchard 1891:424-428
- Hymenolepis siberica* von Linstow 1905. See von Linstow 1905:6-7.
- Hymenolepis spherophora* (Rudolphi 1810) Fuhrmann 1906
- Hymenolepis sagitta* Rossetter. 1906. See Rossetter 1906:275

*Hymenolepis trichorhynchus* Yoshida 1910. See Yoshida 1910:241

*Hymenolepis trichodroma* Fuhrmann 1908. See Fuhrmann 1908:80

*Hymenolepis tenerrima* (von Linstow 1882). See von Linstow 1882:21.

*Hymenolepis fuliginosa* (Krabbe 1882). See Krabbe 1882:355

*Hymenolepis vallei* (Stossich 1892) Fuhrmann 1906. See Stossich 1892:68-69.

*Hymenolepis megalorhyncha* (Krabbe 1869). See Cohn 1901:270

*Hymenolepis* (*Drepanidotaenia*) *podicipina* Szymanski 1905.

See Szymanski 1904:342-344, (Fig. 1-5); 1905:733-734, (Fig. 1-5). The position of the testes in this species is described as follows: "Die drei rundlichen Hoden liegen so dass der eine nahe dem inneren Ende des Cirrusbeutels, die beiden anderen, der eine über dem anderen, an der entgegengesetzten Seite liegen (Fig. 3, 5, tes.)." This species should be restudied and the constancy of this position determined. It is probable that this characteristic position, if constant, may serve to distinguish this form as another genus distinct from those defined above.

*Echinocolyle uralensis* Clerc 1902.

See Clerc 1903:315-317, (Fig. 28, 32, 34, 37, and 89). The position of the testes of this species is described as follows (p. 316): "Les trois testicules sont dorsaux et disposés d'une manière particulière; les deux testicules marginaux (Pl. 9, fig. 34; Pl. 10, fig. 38) se trouvent plus en avant que le troisième qui est médian. Cette position est déjà bien accusée dans les proglottis ayant des organes femelles à peine ébauchés; elle s'accroît encore quand la vésicule séminale et le réceptacle séminal sont gonflés." The description and figures indicate that this is a very characteristic pattern of testes arrangement, but the material should be re-examined before a separate genus is defined.

The following species are closely related to *E. uralensis* in the arrangement of the testes.

*Hymenolepis clausa* von Linstow 1906.

See von Linstow 1906a:177-178 (Figs. 22-23)

*Hymenolepis terraereginae* Johnston 1911.

See Johnston 1911-89 (Figs. 25-26)

*Hymenolepis fasciata* (Rudolphi 1810).

See Krabbe 1869:300 (Figs. 156, 157) (*Taenia fasciata*); Stiles 1896:37-38, (Figs. 56-79) (*Drepanidotaenia fasciata*; Cohn 1901:320; Clerc 1903:307 (*Drepanidotaenia fasciata*))

## XII. SUMMARY

1. A revision of the genus *Hymenolepis* is made on the basis of the arrangement of the testes, and a division of the species assigned to it into three genera.
2. The patterns of testes arrangement serve as reliable generic characters because:
  - (a) they are invariably in the same relative positions with reference to each other in all of the proglottids of the strobila of species having a constant arrangement, and
  - (b) the compound nature of the testes indicates that cestodes having the same pattern of arrangement are closely related since it is believed that in the phylogeny of the group several (two to four) testes became definitely localized in the proglottid and afterwards united, resulting in the compound testes with the different patterns of arrangements found in the present species. The evidence for the compound nature of the testes is presented under the following topics:
    - (1) the irregularities in the number and branching of the vasa efferentia in five species;
    - (2) the lobing of the testes;
    - (3) the irregularities in the number and position of the testes in one species.
3. Fourteen new species belonging to the family are described.

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### EXPLANATION OF PLATES

All of the drawings were made with the aid of a camera lucida, and the details filled in at the same magnifications. In drawings of cross sections the excretory vessels have been indicated by heavy lines and the nerve cord filled in solid.

#### ABBREVIATIONS USED

<i>c</i>	cirrus
<i>cs</i>	cirrus sac
<i>st</i>	seminal receptacle
<i>sv</i>	external seminal vesicle
<i>t</i>	testis
<i>ut</i>	uterus
<i>vag</i>	vagina

PLATE I

## PLATE 1

1. *Weinlandia microcirrosa*. Vasa efferentia from four consecutive proglottids.  $\times 48$
2. *Weinlandia macrostrobilodes*, vasa efferentia from seven consecutive proglottids.  $\times 150$
3. *Weinlandia macrostrobilodes*, vasa efferentia from consecutive proglottids of another specimen than those in figure 2.  $\times 123$
4. *Weinlandia corvi*, vasa efferentia from three proglottids in the same strobila.  $\times 333$

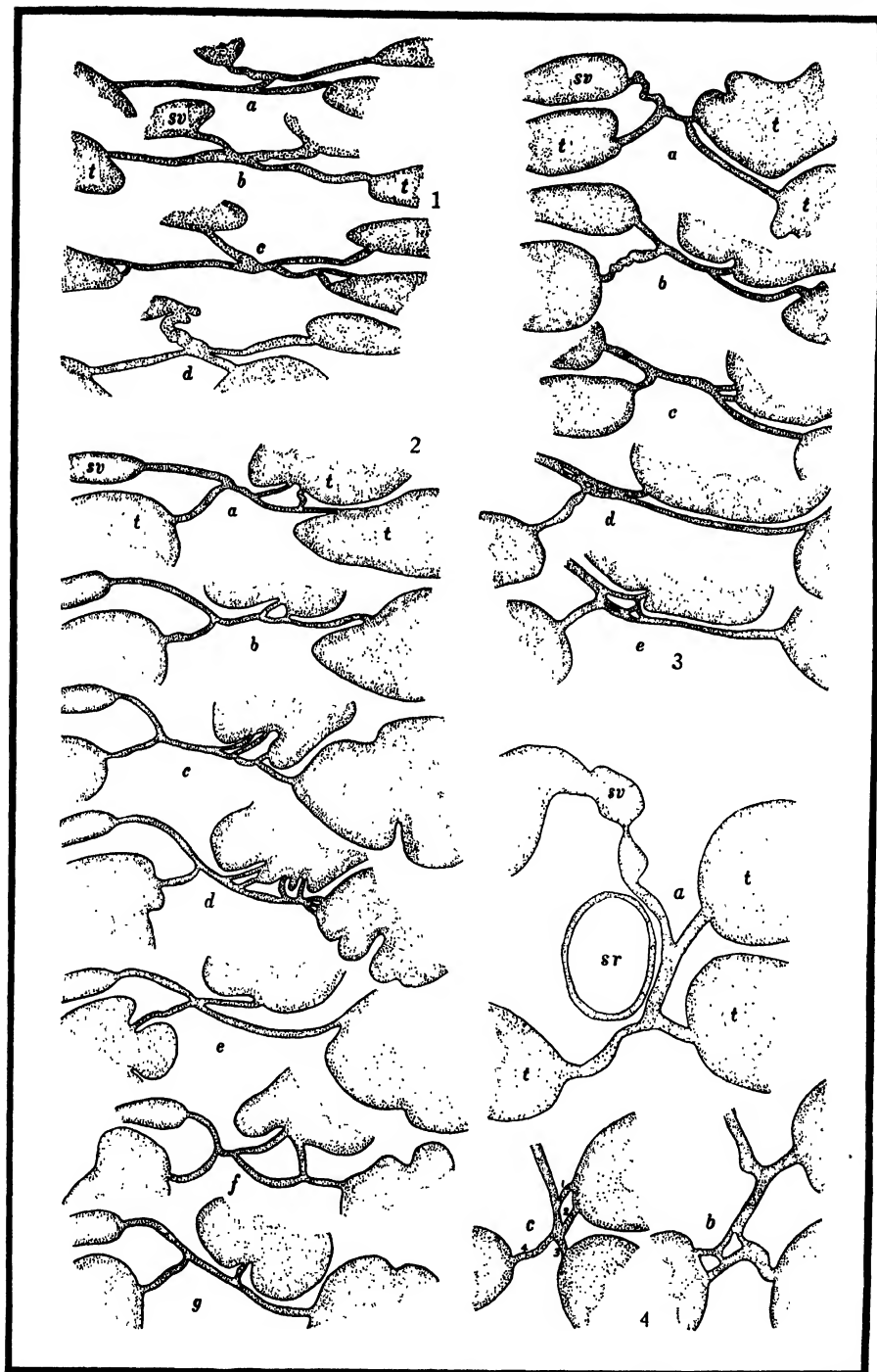


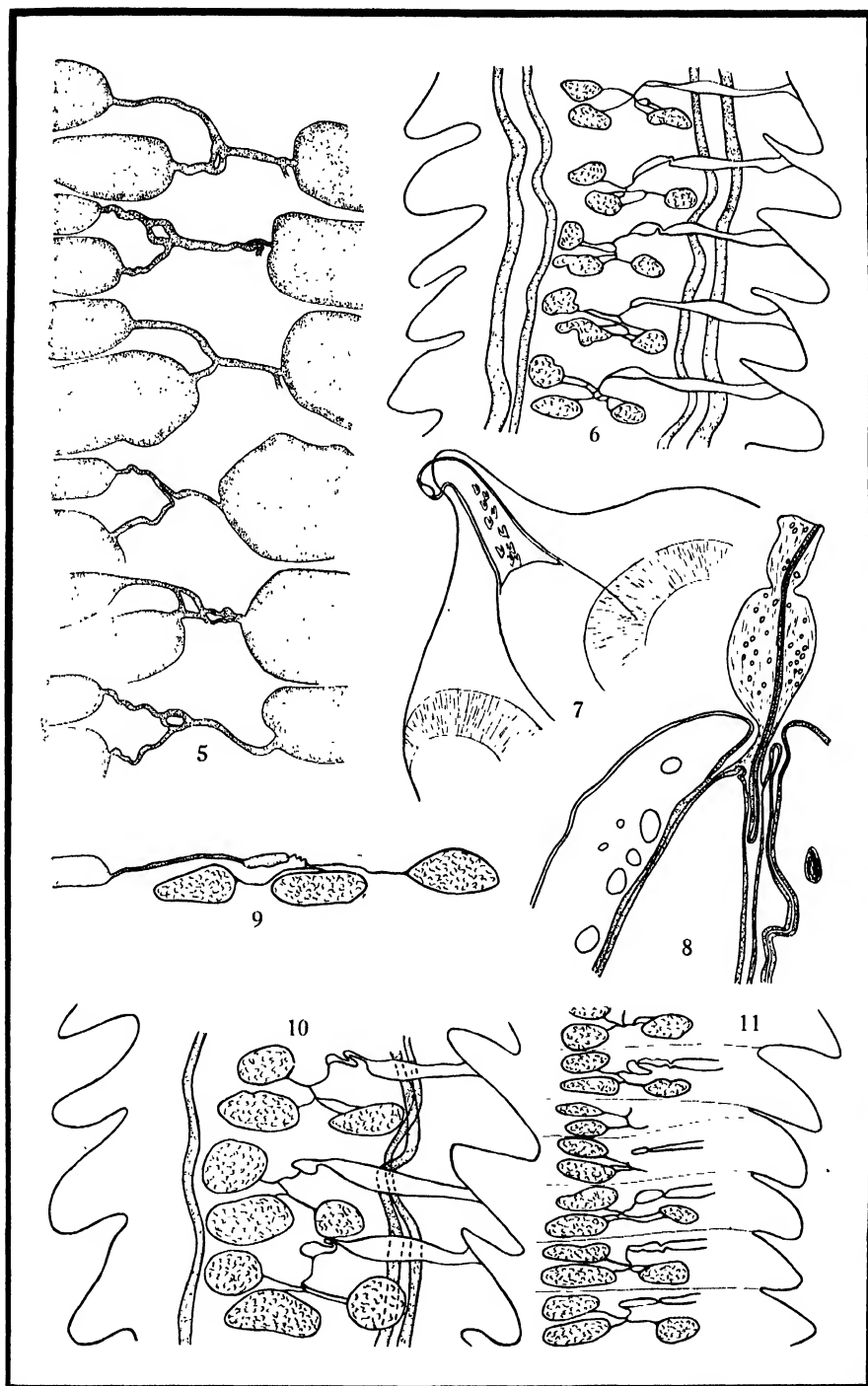




PLATE II

## PLATE 2

5. *Hymenolepis sacciperium*, vasa efferentia from six consecutive proglottids.  $\times 123$
6. *Weinlandia planestici*, five consecutive proglottids.  $\times 80$
7. *Hymenolepis lobulata*, retracted rostellum.  $\times 80$
8. *Wardium fryei*, extruded cirrus.  $\times 33$
9. *Hymenolepis cuneata*, testes and vasa efferentia.  $\times 47$
10. *Weinlandia planestici*, three consecutive proglottids.  $\times 123$
11. *Weinlandia planestici*, seven consecutive proglottids.  $\times 80$



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PLATE III

## PLATE 3

12. *Oligorchis longivaginosus*, drawing showing location of organs in transverse section.  $\times 160$
13. *Oligorchis longivaginosus*, scolex with incomplete set of hooks.  $\times 50$
14. *Oligorchis longivaginosus*, three consecutive proglottids showing variations in teste : arrangement.
15. *Oligorchis longivaginosus*, frontal view of organs from toto mount.  $\times 80$
16. *Oligorchis longivaginosus*, hook.  $\times 355$
17. *Wardium variabile*, transverse section.  $\times 125$
18. *Wardium variabile*, scolex.  $\times 160$
19. *Wardium variabile*, hook.  $\times 600$
20. *Wardium variabile*, uterus from frontal section.  $\times 80$
21. *Wardium variabile*, cirrus sac from frontal section.  $\times 270$
22. *Wardium variabile*, showing position of organs in frontal section.  $\times 80$
23. *Wardium variabile*, excretory system in frontal section.  $\times 125$

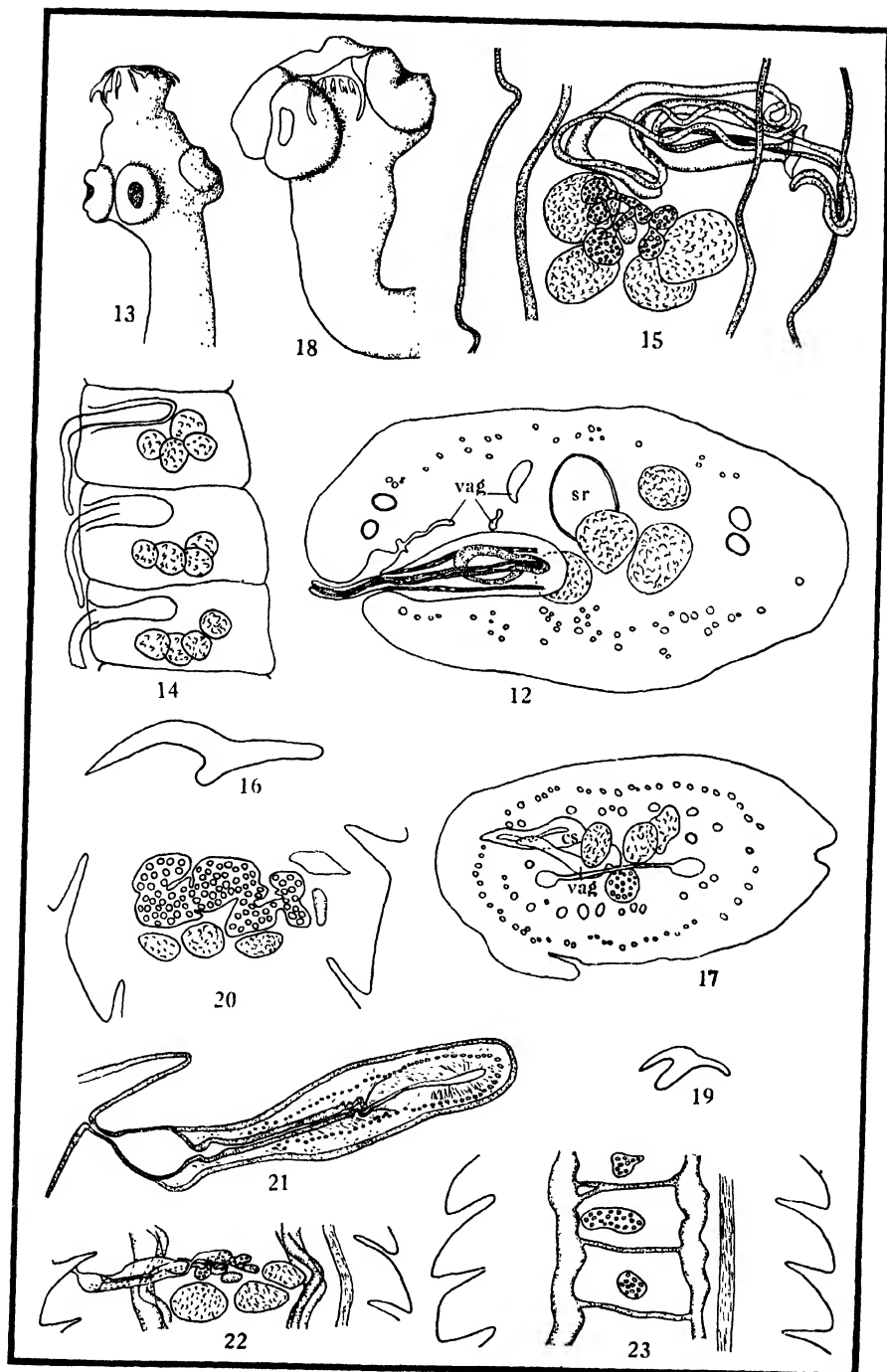






PLATE IV

## PLATE 4

24. *Wardium fryei*, testes arrangement in nine consecutive proglottids.  $\times 50$
25. *Wardium fryei*, egg.  $\times 485$
26. *Wardium fryei*, scolex.  $\times 195$
27. *Wardium fryei*, hook.  $\times 750$
28. *Wardium fryei*, drawing of organs from several frontal sections, ventral view.  $\times 140$
29. *Wardium fryei*, cirrus sac and vagina in transverse section.  $\times 140$
30. *Wardium fryei*, transverse section showing course of uterus.  $\times 25$
31. *Wardium fryei*, transverse section showing testes, ovary, and vitelline gland.  $\times 140$
32. *Hymenolepis lobulata*, transverse section.  $\times 50$
33. *Hymenolepis lobulata*, cirrus sac and vagina in transverse section.  $\times 150$
34. *Hymenolepis lobulata*, scolex.  $\times 50$
35. *Hymenolepis lobulata*, hook.  $\times 450$
36. *Hymenolepis lobulata*, egg.  $\times 300$
37. *Hymenolepis lobulata*, rostellum.  $\times 160$
38. *Hymenolepis lobulata* female reproductive organs from frontal section.  $\times 100$
39. *Hymenolepis lobulata*, male organs in frontal section.  $\times 40$

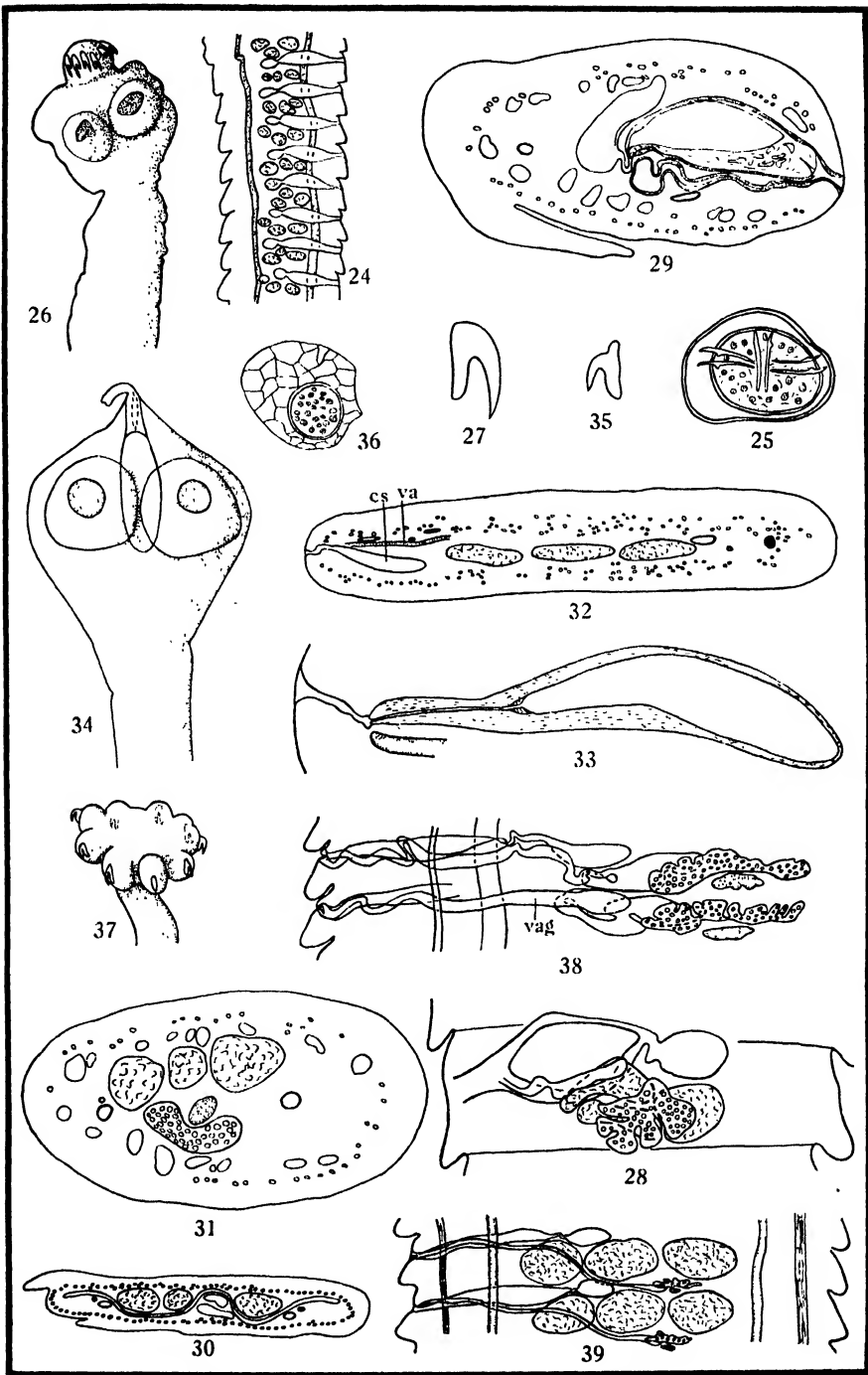
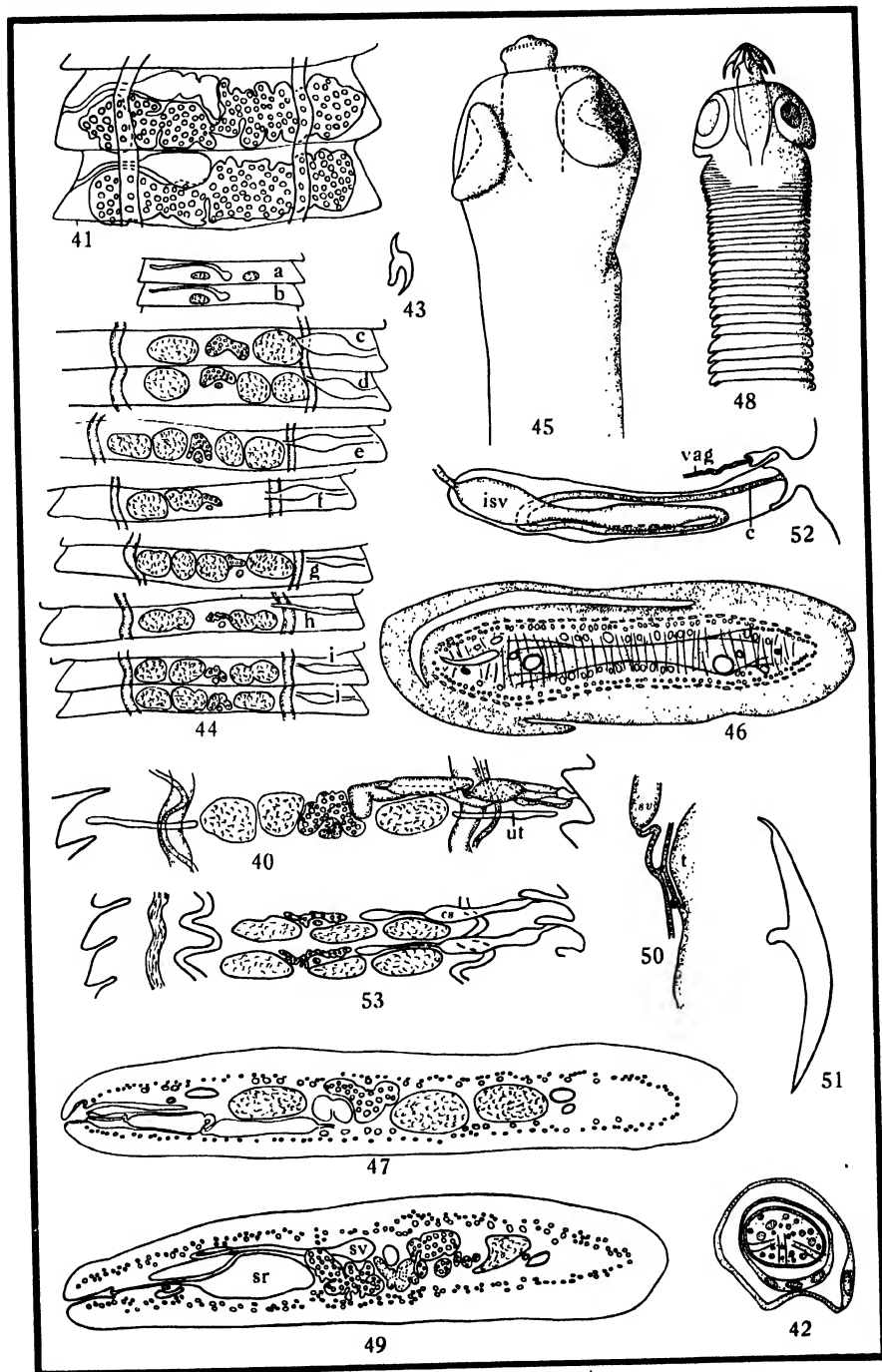




PLATE V

## PLATE 5

40. *Hymenolepis saccipherium*, from frontal sections.  $\times 40$
41. *Hymenolepis saccipherium*, uterus.  $\times 25$
42. *Hymenolepis saccipherium*, egg.  $\times 350$
43. *Hymenolepis saccipherium*, hook.  $\times 500$
44. *Hymenolepis saccipherium*, a series of proglottids, a-b from one strobila, c-j from another, showing variations in the number and arrangement of the testes.
45. *Hymenolepis saccipherium*, scolex.  $\times 125$
46. *Hymenolepis saccipherium*, transverse section showing arrangement of musculature.  $\times 50$
47. *Hymenolepis saccipherium*, reproductive organs in transverse section.  $\times 50$
48. *Hymenolepis cuneata*, scolex.  $\times 50$
49. *Hymenolepis cuneata*, reproductive organs in transverse section.  $\times 25$
50. *Hymenolepis cuneata*, vasa efferentia from one proglottid in frontal section.  $\times 155$
51. *Hymenolepis cuneata*, hook.  $\times 350$
52. *Hymenolepis cuneata*, cirrus sac.  $\times 80$
53. *Hymenolepis cuneata*, from frontal sections showing position of organs.  $\times 25$





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PLATE VI

## PLATE 6

54. *Weinlandia lateralis*, a proglottid toward the anterior end of the strobila.
55. *Weinlandia lateralis*, hook.  $\times 730$
56. *Weinlandia lateralis*, scolex.  $\times 115$
57. *Weinlandia lateralis*, transverse section of a proglottid showing course of uterus.  $\times 50$
58. *Weinlandia lateralis*, from section of proglottid farther posterior than shown in figure 54.  $\times 50$
59. *Weinlandia lateralis*, transverse section toward the anterior end of strobila.  $\times 95$
60. *Weinlandia lateralis*, transverse section farther posterior than figure 59.  $\times 50$
61. *Weinlandia lateralis*, uterus in proglottid toward posterior end of strobila.  $\times 25$
62. *Weinlandia lateralis*, vasa efferentia.  $\times 330$
63. *Weinlandia macrostrobilodes*, section of scolex showing arrangement of muscles.  $\times 330$
64. *Weinlandia macrostrobilodes*, uterus.  $\times 15$
65. *Weinlandia macrostrobilodes*, hook,  $\times 500$
66. *Weinlandia macrostrobilodes*, egg.  $\times 330$
67. *Weinlandia macrostrobilodes*, scolex.  $\times 155$
68. *Weinlandia macrostrobilodes*, proglottids from anterior end of strobila.  $\times 25$
69. *Weinlandia macrostrobilodes*, transverse section showing course of uterus.  $\times 40$ .
70. *Weinlandia macrostrobilodes*, reproductive organs in toto.  $\times 25$
71. *Weinlandia macrostrobilodes*, reproductive organs in toto farther anterior than figure 70.  $\times 40$

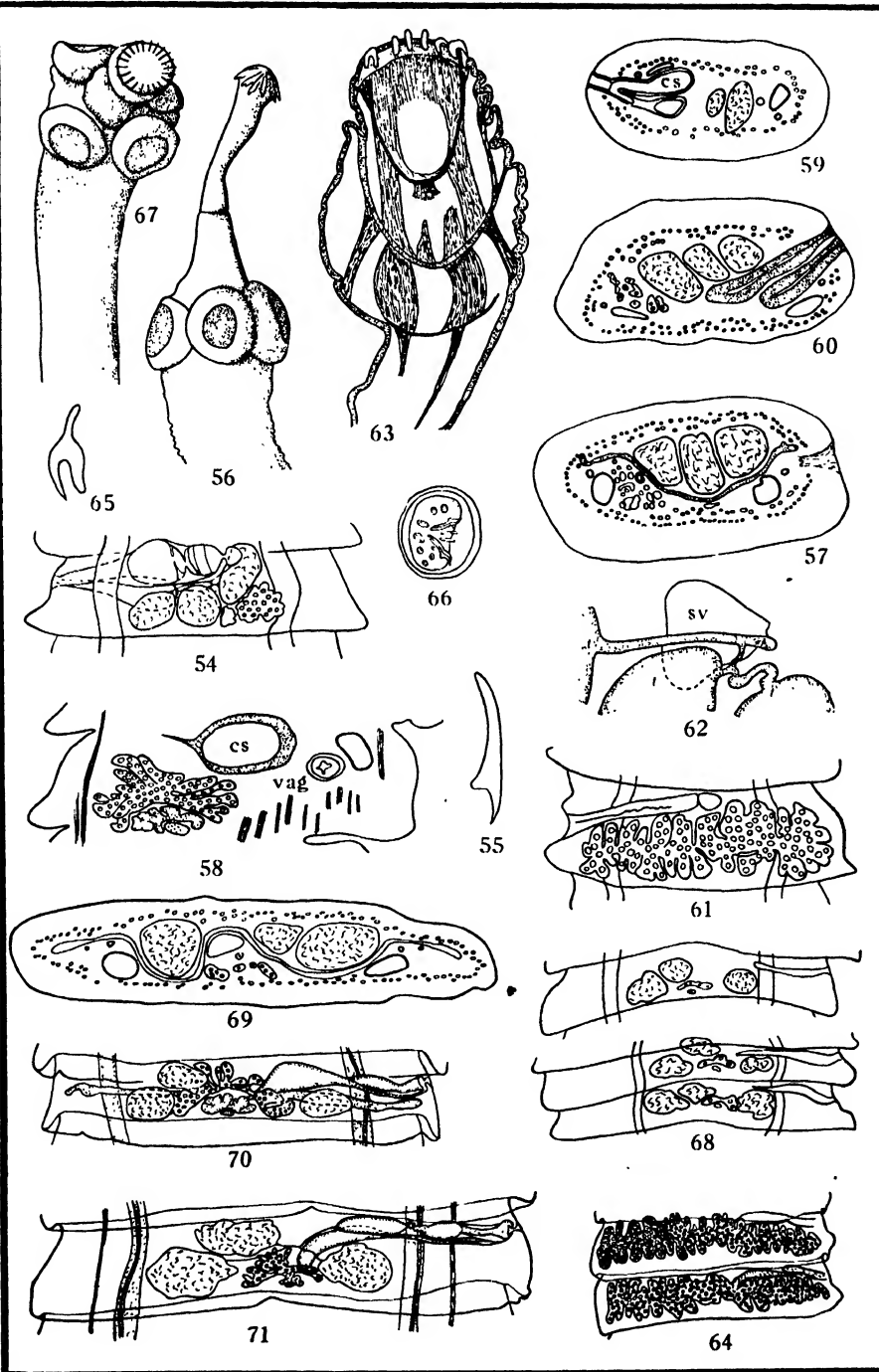
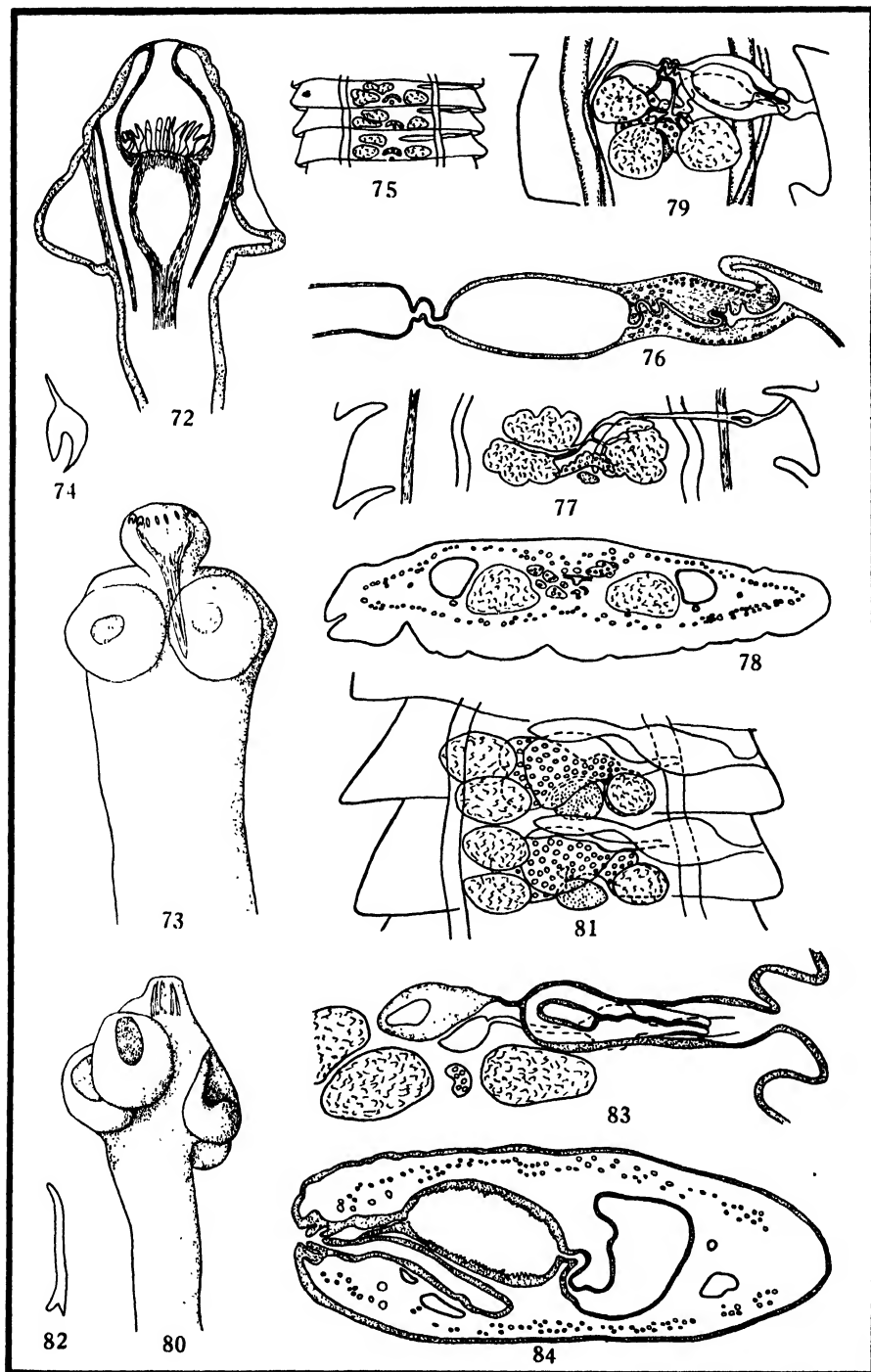




PLATE VII

## PLATE 7

- 72. *Weinlandia introversa*, section of scolex showing arrangement of muscles.  $\times 330$
- 73. *Weinlandia introversa*, scolex in toto.  $\times 160$
- 74. *Weinlandia introversa*, hook.  $\times 750$
- 75. *Weinlandia introversa*, proglottids from anterior portion of strobila.  $\times 25$
- 76. *Weinlandia introversa*, cirrus sac.  $\times 50$
- 77. *Weinlandia introversa*, reproductive organs from toto mount.  $\times 80$
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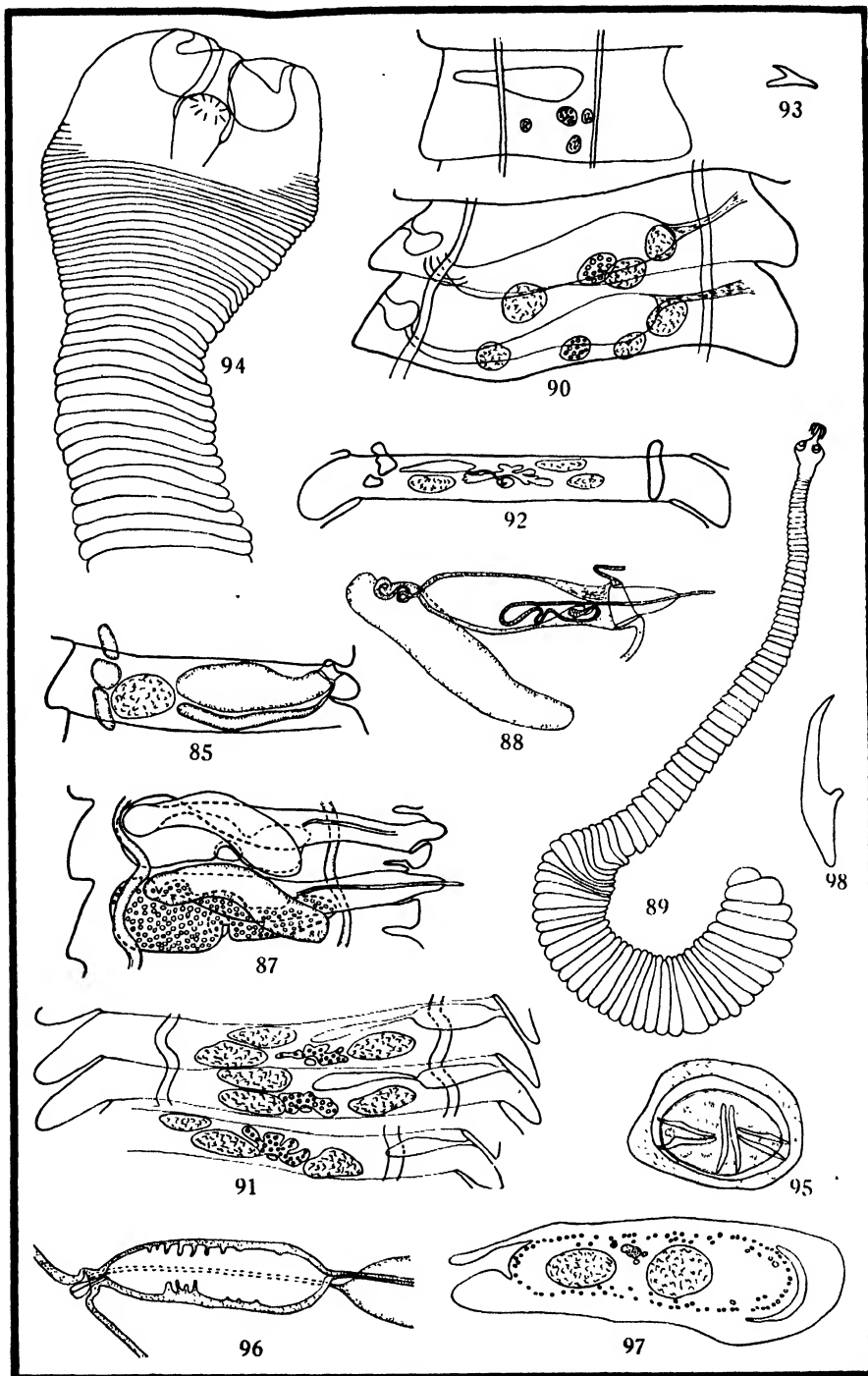
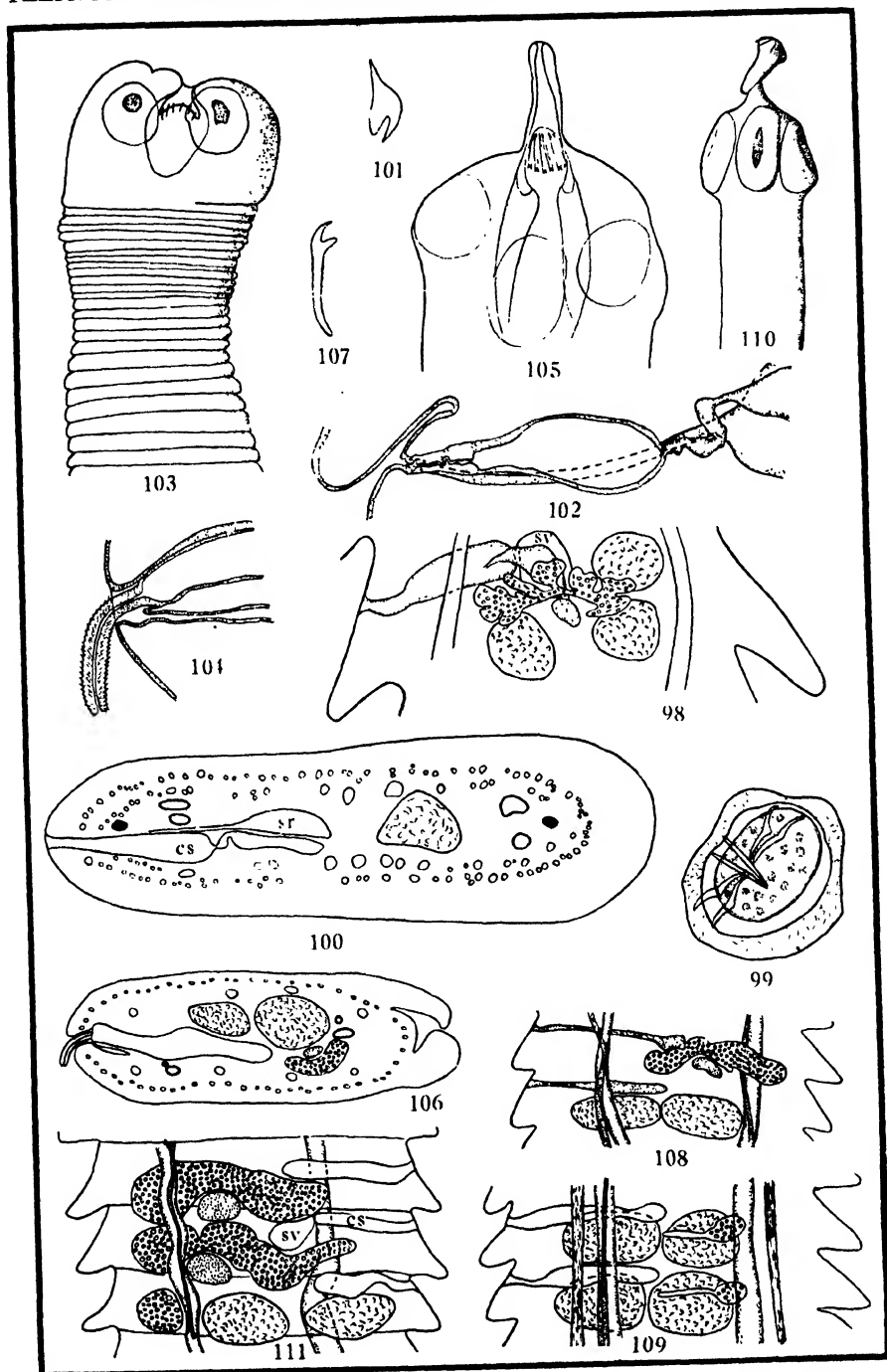




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# **SOME NORTH AMERICAN FISH TREMATODES**

**WITH 6 PLATES, 2 CHARTS AND 1 TEXTFIGURE**

**BY**

**HAROLD WINFRED MANTER**

**Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward  
No. 287**

**THESIS**

**SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE  
SCHOOL OF THE UNIVERSITY OF ILLINOIS**

**1925**

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## INTRODUCTION

The study of the parasites of North American fish, especially marine species, offers a comparatively new field to the investigator. Linton has opened this field in a broad sense by his papers on fish parasites of the Woods Hole region and of the Atlantic waters of Southern United States. This pioneer work has been necessarily incomplete in some respects. On the parasites of fishes inhabiting the colder waters of the northern Atlantic, almost no work has been done in America. Stafford and Cooper have made small collections in these regions. On European shores considerably more research has been done, and here the early work of Van Beneden, Olsson, and Levinsen has been followed by valuable contributions from Looss, Odhner, Lebour, Nicoll, and others.

The present paper is based very largely upon studies of marine fish parasites from the Maine coast. These studies were first undertaken at the Mount Desert Island Biological Laboratory during the summer of 1924, although some material was also collected in the same region in 1923. Early in the work of collection, attention was directed to a common trematode (*Otodistomum cestoides*) of the barn-door skate. Considerable time was devoted to the structure of this form and its life history. Later, a large series of fresh-water forms related to this species were also studied and compared. A brief report of the trematodes collected from marine fish has already been published (Manter, 1925).

Sincere appreciation is here extended to Professor Ulric Dahlgren for the use of the laboratory facilities at the Mount Desert Island Biological Station. Acknowledgment is also rendered to the Hygienic Laboratory of the U. S. Public Health Service and to the U. S. National Museum for the loan of valuable material. Above all, is the writer indebted to Dr. Henry B. Ward, under whose direction these studies were undertaken. To him appreciation is extended, not only for his constant interest, but also for the loan of material from his personal collection of parasites, and for the use of his extensive library. To others, who, like fellow-students, have been less intimately associated with this work, but who have gladly cooperated in many ways, gratitude is likewise expressed.

## MATERIAL AND METHODS

The collection of parasites was not limited to any particular group. In general, a broad collection of metazoan fish parasites was attempted. The final collection included trematodes, cestodes, nematodes, acantho-

cephala, copepods, leeches, an ectoparasitic turbellarian, and an ectoparasitic isopod. From this collection the trematodes were chosen for special study.

The most common shore fish such as sculpin, flounder, herring, and skates were obtained from Frenchman's Bay in the immediate vicinity of the Laboratory. Most of the fish examined, however, were obtained at the small fishing village of Manset on the south side of Mount Desert Island. Here specimens of the larger food fish such as cod, haddock, and hake were available in large numbers. Identification of the host was usually simple as most of the fish examined were common and well known species. Some uncertainty was unavoidable in the correct identification of a few forms, such as the sculpins.

The following table (Table 1) shows the general occurrence of the different groups of parasites according to hosts.

TABLE 1  
GENERAL DISTRIBUTION OF ENTOZOA IN HOSTS EXAMINED

Name of Host		Number of Hosts				
Scientific	Common	Examined	With Trematodes	With Nematodes	With Cestodes	With Acanthocephala
<i>Acanthias vulgaris</i>	Common dog fish	12		2	12	
<i>Raia erinacea</i>	Bonnet skate	8	1	1	8	
<i>Raia diaphanes</i>	Big skate	2			2	1
<i>Raia stabuliforis</i>	Barn-door skate	20	18	7	20	
<i>Raia scabrata</i> (?)	Skate	1		1	1	
<i>Anguilla chrysypa</i>	Common eel	2				2
<i>Clupea harengus</i>	Herring	28	9	6		
<i>Osmerus mordax</i>	Smelt	5	3	2		
<i>Scomber scombrus</i>	Mackerel	5		5		
<i>Fundulus heteroclitus</i>	Killifish, minnow	25	9		6	23
<i>Tautoglabrus adspersus</i>	Cunner	4		3		1

TABLE 1 (continued)

Name of Host		Number of Hosts				
Scientific	Common	Examined	With Trematodes	With Nematodes	With Cestodes	With Acanthocephala
<i>Myxocephalus octodecimspinosus</i>	Sculpin	11	3	7	4	9
<i>Pholis gunnellus</i>	Butterfish	9	2			
<i>Anarrhichas lupus</i>	Wolf-fish	2	1	1		
<i>Zoarces anguillar</i>	Eel pout	1				1
<i>Pollachius virens</i>	Pollack	4	2	3		2
<i>Gadus callarias</i>	Cod	10	8	9	2	10
<i>Melanogrammus aeglefinus</i>	Haddock	17	4	9	5	17
<i>Urophycis tenuis</i>	Hake	3	3	1	1	2
<i>Urophycis chuss</i>	Squirrel hake	6	5	6	1	4
<i>Hippoglossus hippoglossus</i>	Halibut	2	1	2		2
<i>Pseudopleuronectes americanus</i>	Flounder	19	3	3	2	15
<i>Limanda ferruginea</i> (?)	Sand dab	2		2	2	1
Total		198	72	70	66	90

The barn-door skate (*Raia stabuliforis*) was found to furnish the most varied and interesting parasites. Ecto-parasitic on this skate were found; *Micropharynx parasitica* (a tri-clad turbellarian), *Aega psora* (an isopod), and a large leech, *Oxyostoma typica*.\* In the nasal cavity was found *Charopinus dalmanni* (Retz.) a large parasitic copepod. The stomach was usually heavily infected with the trematode, *Otodistomum cestoides*. Large numbers of cestodes occurred in the spiral valve. Although only a part

\* For the identification I am indebted to Prof. J. Percy Moore who reports that the leeches "are representatives of *Oxyostoma typica* Malm or possibly a closely related species of the same genus."



of this cestode material was examined, two forms were identified as *Rhynchobothrius erinaceus* (van Ben.) and *Acanthobothrium coronatum* (Rud.).

One interesting case of Acanthocephalan infection was found in *Fundulus heteroclitus*. The livers of these minnows were almost invariably heavily infected with a juvenile form of *Neoechinorhynchus*. These parasites were sometimes free in the liver tissue but usually were coiled in a very thin-walled cyst. In one liver 25 or 26 such cysts could be counted. Only two of about 25 specimens failed to show the cysts macroscopically. In one case, this same form of juvenile Acanthocephalan was found in the intestine. This possible occurrence of the parasite in the intestine led to feeding experiments. A *Fundulus* was isolated and fed liver containing cysts from other minnows. As some of the material was disgorged, it could not be ascertained exactly how many cysts were ingested. The fish was fed again on the following day, and killed and examined on the third day. Three of the Acanthocephala were found in the intestine. This experiment was repeated by again feeding an isolated *Fundulus* the cysts on two days, and examining it on the third day. This second fish contained six of the Acanthocephala in its intestine. It is evident that the parasite can be transmitted from the liver to the intestine of the same species host. A possible explanation of the rare occurrence of this type of transfer in nature is found in the fact that the viscera of dead minnows in the aquaria are readily devoured by the other minnows. No evidence was found that the parasite ever reaches sexual maturity in this host.

The final host of the parasite was found to be the common eel, *Anguilla chrysypa*. The locality from which the minnows were caught harbored numerous eels. Two of these fish were caught and examined for parasites. The first contained large numbers (about 50) of a *Neoechinorhynchus* in the lower part of the intestine. The parasites were apparently identical with the young form taken from the minnow, differing only in being sexually mature. The second eel contained three minnows in the stomach. One of these minnows was practically digested. From the stomach content in this region one of the Acanthocephalan cysts was recovered. Furthermore, there was found free in the upper part of the intestine one of the juvenile Acanthocephalans without the cyst. Lower down in the intestine occurred large numbers of the adult parasite attached to the intestine wall. The species of Acanthocephala was kindly identified by Dr. H. J. Van Cleave as *Neoechinorhynchus cylindricus* (Van Cleave).

The demonstration seems to be quite complete that the eel (at least in this particular locality) acquires (at least in part) its infection through the minnow, *Fundulus heteroclitus*. Whether the minnow is a necessary link in the life-history of the parasite is very doubtful. Van Cleave (1920) in explaining juvenile forms of Acanthocephala encysted in various fish,

suggests that they may result from ingestion of the larva when it is too young to maintain itself in the intestine, the immature larva developing to an infective juvenile form in some tissue outside the digestive tract.

In the course of the present work, no new methods of technique were discovered. The finding of the larger parasites such as most cestodes, acanthocephala, and nematodes is simple. To collect the smaller forms such as many trematodes, the content of the digestive tract of the host must be minutely examined. Best results were obtained by diluting a small amount of material with considerable water in a large glass dish. A changing from light to dark of the background below the dish is often helpful. Careful scraping of the wall of the digestive tract is usually necessary to remove many of the smaller parasites.

Cestodes were killed in  $\text{HgCl}_2$  solution. Agitation by shaking or the actual stretching by hand of cestodes is necessary to prevent excessive contraction. Trematodes were killed according to the Looss method (Looss 1901) by first shaking in water and then in a 50% solution of  $\text{HgCl}_2$ . A modified Gilson's solution (Petrunkevitch solution) was also found very satisfactory for trematodes. Nematodes were killed by placing in hot 70% alcohol or hot Petrunkevitch solution. Acanthocephala from the marine fish were first placed in fresh water which causes complete extension of the proboscis. When the Acanthocephala no longer respond to stimuli they are removed to the killing solution.

Some difficulty was experienced by some forms, especially trematodes, later becoming quite black, due apparently to a precipitation of metallic mercury. This condition might be due to insufficient or delayed treatment with iodized alcohol. A semisatisfactory method of reclaiming such specimens was found to consist of treating them with a weak solution of nitric acid. The acid removes the mercury but slightly stains the tissues.

In staining trematodes for total mounts, Ehrlich's or Delafield's hematoxylin or a mixture of the two was found to be very satisfactory. Alum cochineal also gave good results. Sections were stained with the ordinary reagents such as hematoxylin, iron hematoxylin, safranin, eosin, orange G, and Lyon's blue.

The present studies can be divided into three rather distinct parts as follows. First, an intensive study of *Otodistomum cestoides*, its first larval form, its growth changes within the final host, and its morphology. Some data was also obtained from an attempt to trace the life history of this form. Second, a comparative study of the entire family of the Azygiidae, and a revision of the American representatives of the genus *Azygia*. Third, a briefer account of each of the other forms of marine trematodes in the collection. This last account also includes data on several forms from the collection of Dr. H. B. Ward. These latter were collected from the Woods Hole region.

## HISTORICAL SURVEY

Van Beneden (1858 and 1871) was one of the earliest workers to deal particularly with fish parasites and many of the more common species were first described by him. His collections were made along the coast of Belgium. Olsson in 1868 records 32 different trematode parasites from Scandinavian fish. Twenty-seven of these parasites were distomes, and eight were reported as new. Olsson's work covered a wide host range, the trematodes being collected from 42 different species of fish.

Levinsen published in 1881 results of his studies on trematodes of arctic fish. This work is the product of two years spent on the west coast of Greenland and constitutes the first comprehensive record of trematodes from strictly arctic marine fish. The number of host species examined was small (six), but the trematode fauna of a few fish such as the sculpin was thoroughly studied. Nine different species of trematodes were recorded from this host. Levinsen lists thirteen different sexually mature forms, most of which are distomes. Seven species are described as new.

Early work on the fish trematodes of the Mediterranean was done by Rudolphi, Monticelli, Stossich, and Looss. The detailed and accurate morphological observations of Looss have been of special service, and his (1899) conception of the genus among distomes has resulted in a complete systematic reorganization of that group.

Probably the most important paper on trematodes of arctic fish is Odhner's contribution (1905) to the *Fauna Arctica, Trematoden des arktischen Gebietes*. This critical monograph of the arctic trematode fauna is not limited to fish parasites but includes a few forms from avian and mammalian hosts. Odhner also restudied Levinsen's material. As the paper deals with considerable change in the "natural system" of trematodes, short descriptions are given of some forms outside the arctic regions. Twenty-two different trematodes, 19 of which are Digenea, are recorded from fish. Among these fish trematodes, four new genera and three new species are described. Several previously known species are redescribed, and some important systematic reorganizations are made. In a series of later short papers under the general title, *Zum natürlichen System der digenen Trematoden*, Odhner has made numerous subsequent additions to our knowledge of relationships among the trematodes, and his conclusions have been largely accepted by Nicoll (1915) and others.

The trematodes of the British marine fish are probably better known than those of any other particular region. This is largely due to the researches of Lebour, Johnstone, T. Scott, A. Scott, and Nicoll. According

to Nicoll, up to 1915 nearly 100 species of trematodes had been recorded from British marine fish. Nicoll's (1915) list of trematodes from marine fish contains 241 different species of trematodes belonging to 119 genera. Of these trematodes, 157 species and 73 genera are distomes.

In America the work of Linton at Woods Hole, Beaufort, N. C., and the Tortugas stands almost alone. The last named region is especially interesting in revealing a very rich and varied trematode fauna (Linton 1911) with forms differing considerably from most of the more northern forms. Stafford (1904) gives a list of 37 trematodes from 32 different Canadian marine fish. Cooper (1915) gives more complete data on a few forms from the same region.

A large amount of the literature is, of course, in the nature of special studies on individual or few forms. Examples of papers of this type are found in the works of Poirier (1885), Villot (1879), Pratt (1898), Darr (1902), Buttel-Reepen (1903), and Mühlenschlag (1914).

## THE MORPHOLOGY OF OTODISTOMUM CESTOIDES

## OTODISTOMUM CESTOIDES (VAN BENEDEN 1871)

*Otodistomum cestoides* (van Ben.)

Syns.: *Distomum cestoides* van Ben. 1871

*Otioidistomum veliporum* of Stafford 1904

*Otioidistomum veliporum* of Lebour 1908

*Otioidistomum veliporum* of Lönnberg 1891

From stomach, *Raia stabuliformis* (= *R. laevis*)

Reported hosts: *Raia batis*

*Raia laevis*

*Raia fullonica*

*Raia lintea*

*Raia clavata*

*Raia radiata*

*Raia macrorhyncha*

*Chlamydoselache anguinea*

*Dist. cestoides* was first obtained by van Beneden (1871) from *Raia batis*. The genus *Otodistomum* was named by Stafford (1904) for a form he obtained from the stomach of *Raia stabuliformis* (= *R. laevis*). This form he called *Otodistomum veliporum*, identifying it as the *Dist. veliporum* of of Creplin. The close resemblance between the two species *cestoides* and *veliporum* has been a cause of general confusion, and, indeed, the two have been considered synonymous. Odhner (1911b) first showed that *O. cestoides* (van Ben.) had been incorrectly identified as *O. veliporum* by previous workers including Stafford, Lebour, and Lönnberg. In the course of the present studies both species were available for comparison. Specimens of *O. veliporum* were obtained from the collection of Dr. H. B. Ward\* and were collected by him from *Raia binoculata* in Alaska in 1909. Further material of this same form was collected by a fellow-student from the same host at Friday Harbor, Washington, in 1924. Frequent reference will be made to this species in connection with the following discussion of the morphology of *O. cestoides*.

The host records of the two species are doubtless somewhat confused. According to the literature, *O. veliporum* appears to have a much wider host range among the Selachians, *O. cestoides* being almost entirely restricted to *Raia* species. In the region of Mount Desert Island *O. cestoides* occurs abundantly in *Raia stabuliformis*, but was never found in any other species of skate. Both Stafford and Cooper report it from Canadian waters.

\* Collection of Dr. H. B. Ward, vial No. 48a from Excursion Inlet, Alaska, July 22, 1909.

Linton also records it from Woods Hole but there it seems to be a rare parasite.

The trematode was found in the lower part of the pyloric stomach of *Raia stabuliforis*. It is one of the most common fish trematodes in the region of Mount Desert Island as almost all the skates of this species we re-infected, sometimes heavily. Only two individuals among twenty examined in 1924 were uninfected, while all of the several examined in 1923 contained the trematode. The average degree of infection is about 21, although the number varies from only 2 or 3 to about 150. In a number of cases only young immature forms were found. It is also common, especially if the infection is light, to find only mature forms or at least no very young specimens. Several instances were found wherein all stages were present. Table 2 shows a record of the collection of this parasite.

The trematode is one of the largest known. Stafford records worms as long as 80 mm. when extended. There is a remarkable size variation. The longest specimen in the present collection measured about 65 mm., while several were found only 2 or 3 mm. in length. Sexual maturity is reached when the worm has a length of about 11 mm.

The body form is elongate and somewhat flattened dorso-ventrally especially in the posterior region. The anterior end tapers slightly in front of the ventral sucker and is bluntly pointed. Behind the ventral sucker the body tapers only very gradually and the posterior end is usually blunt. In some cases, however, when the worm is extended the posterior tip is sharply pointed. In this case, the body form is spindle-like.

The two suckers are close together near the anterior end. The ventral sucker is the larger and very powerful. When in use this ventral sucker may be protruded from the body very prominently. The worms cling tenaciously by means of the ventral sucker and may extend the anterior end of the body for some distance, feeling about in a leech-like manner. When removed from their host the worms cling to each other by means of their ventral suckers, and it is often difficult to separate individuals after they have become attached in this manner. There is a marked tendency for the worms to bend slightly inward, (i.e., ventrad), so that in profile they assume a curved or crescentic shape. This shape is especially marked when the trematodes are killed unless they are prevented by some mechanical means from so curling. The color of the worms is a translucent white when alive, becoming opaque white when killed. The region of the uterus just posterior to the ventral sucker is dark brown in color, due to the presence of many eggs which possess a light brown shell.

The oral sucker is smaller than the ventral sucker and the size ratio of the two does not show any progressive change with growth, averaging the same in very small individuals as it does in the largest. The anterior sucker averages slightly over .6 the size of the ventral one, or a proportion of

TABLE 2  
INDIVIDUAL INFECTION OF *Raia stabuliforis* WITH *Otodistomum cestoides*

Date	Content of Stomach	Number of parasites	Condition
July 16	Empty	Several	Mostly mature
	Sculpin	"	
" 27	Empty	None	
August 5	Empty	Few	Immature
	"	"	"
	"	8-10	
	"	30-35	
	"	15-20	
	"	10-15	
" 8	Crab, shrimp	16-20	Mature
	Remains of flounder	16	Small, immature
" 12	3 herring, part of lobster	16-20	Mature
	Empty	17	Small
	"	4-5	
" 19	"	Many	All sizes, 10 or more mature
	8-10 small crabs, shrimp	None	
	Empty	12-15	Mostly mature
	"	160-170	Heaviest infection. 100 immature
	Remains of fish, Buccinum	Several	All sizes
" 28	Flounder	2	Mature

about 3 : 5. Odhner (1911b), however, gives a ratio of 3 : 4 for *O. cestoides* and 3 : 5 for *O. veliporum*. Miss Lebour's single specimen with a ratio of 1 : 2 must have been (as Odhner suggests) an abnormal condition. For the measurements of the suckers see Table 4.

The circular opening of the oral sucker may be directed anteriorly, but is usually ventral. The ventral sucker is very deep, extending nearly to the dorsal surface of the body when the worm is extended. The cavity of this sucker extends posteriorly as well as dorsally, a condition due to the

greater development of its muscles in the posterior region. While interesting because of the high degree of muscular development, the structure of the two suckers is like that already described for similar forms by Poirier (1885) and for *O. veliporum* by Mühlschlag (1914).

From the ventral anterior rim of the ventral sucker two muscle bands pass dorsally and can be traced nearly to the longitudinal body muscles of the dorsal wall. Crossing them obliquely a strong band of muscles can be seen to extend ventrally and anteriorly from the central dorsal border of the sucker to the longitudinal muscles of the ventral body wall. There are also muscle fibers extending laterally from this anterior ventral border of the sucker. Muscle bands at the posterior border of the sucker extend laterally on each side, and other bands extend dorsally to the dorsal body wall.

Short muscles are attached to the anterior margin of the oral sucker and course anteriorly and dorsally where they seem to join longitudinal body muscles of the dorsal side. Just posterior to these occur lateral oblique muscles running dorsally and laterally from each side of the sucker. They also are closely related with the dorsal longitudinal body muscles. Some of these fibers extend to the outer edge of the sucker. Finally, from the posterior edge of the sucker oblique muscle bands run dorsally and posteriorly and attach themselves to the pharynx.

The body wall consists of the cuticula, a layer of circular muscles, and a layer of longitudinal muscles (Fig. 12). The cuticula is a thick structureless layer surrounding the entire body. In a specimen about 25 mm. in length, this cuticula was about  $17\mu$  thick on the ventral surface of the neck region and about  $28\mu$  thick on the ventral surface of the posterior region. The thicknesses on the dorsal surfaces of the same regions were 34 and  $37\mu$ . Hence, the same relative thicknesses are found that Mühlschlag noted for *O. veliporum*. For the latter species, Mühlschlag's measurements are all much smaller than were found in the present species, but the size of the specimen was not given in the former case. The cuticula is much thinner over the inner surfaces of the two suckers. Here it measures only 5 to  $8\mu$  in thickness.

The body wall is thrown into circular folds which are more prominent with increased degree of contraction. These folds give the ringed appearance characteristic of this group of trematodes. Sections show that these folds involve the cuticula, and the layer of circular muscles, but not the layer of longitudinal muscles. The thickness of the circular layer, therefore, varies greatly. The layer is very thick in the center of the folds, and is greatly reduced in the furrows between the folds. In the following table a medium condition is represented as far as possible.



THICKNESS OF REGIONS OF BODY WALL  
(Specimen about 25 mm. long)

<i>Ventral Surface</i>			
	Neck Region	Testis Region	Posterior Region
Cuticula	17 $\mu$	28-30 $\mu$	28-30 $\mu$
Circular muscles	40-50	50-55	50-55
Longitudinal muscles	34	17-20	17
<i>Dorsal Surface</i>			
Cuticula	34 $\mu$	40 $\mu$	35-45 $\mu$
Circular muscles	50	50	38
Longitudinal muscles	22	20	16

The parenchyma presents no unusual features. It consists of a spongy tissue, filling in the regions between organs. Small nuclei are common, and also larger cells which are possibly nervous in function. The parenchyma is set through with muscle bands. Many of these, especially near the body wall, and within the neck region are oblique or diagonal, but the majority run in longitudinal bands throughout the length of the body. In species of *Azygia* (a related genus) a very definite and relatively narrow band of these longitudinal muscles occurs. In cross-section, the body is separated by them into medullary and cortical regions. Various *Azygia* species were available for comparison with *O. cestoides* in this respect. The localization of the muscles is much more pronounced and definite in *Azygia* where they form a rather compact layer. Here also the follicles of the vitellaria are outside this layer, that is, in the cortical region. In *Otodistomum*, the longitudinal parenchyma muscles are not limited to such a narrow layer and their formation is much less compact (Fig. 23). The region of their occurrence is, however, definite enough so that it can be noted that the follicles of the vitellaria lie largely internal to them, a condition to be contrasted with that occurring in *Azygia* species.

The nervous system could not be worked out in detail, only its more prominent features being noted. These agreed with data already known for similar forms.

The pharynx is ovoid or egg-shaped. It is located just posterior and slightly dorsal to the oral sucker. Its size is about 0.5 mm. by 0.3 to 0.4 mm. in average sized specimens. The largest examples measured about 0.75 mm. in length. In a specimen 24.5 mm. in length the pharynx measured 0.56 by 0.37 mm., and the thickness of its walls was about 0.18 mm. There is no pre-pharynx and the pharynx itself may protrude slightly into the cavity of the oral sucker. The pharynx usually extends obliquely dorsally and posteriorly. The opening between pharynx and oral sucker is therefore facing obliquely between a dorso-ventral and a postero-anterior direction. The walls of the pharynx are very muscular and show the same sets of muscles found in the suckers. Circular or equatorial muscles are especially

powerful in the posterior region where the esophagus joins the pharynx and these may act as a sphincter muscle between the two (Fig. 10).

Special muscle bands run obliquely forward from the dorsal and ventral sides of the pharynx to the oral sucker. These bands are much more prominent on the ventral side. The degree of contraction of these muscles no doubt accounts for the varying position of the pharynx especially its tip in the dorso-ventral direction in relation to the oral sucker. Sometimes the pharynx entirely overlaps the sucker dorsally and rarely it extends almost directly posteriorly.

The pharynx leads directly into the esophagus. In a specimen about 25 mm. long the antero-posterior length of the unpaired region of the esophagus adjacent to the pharynx is only about  $57\mu$ , but the organ divides immediately into two lateral stems and is actually a tube running laterally and perpendicular to the long axis of the pharynx. The length of each lateral stem is about 0.4 mm. Each stem bends toward the anterior and extends in that direction about 0.3 mm. before opening into the intestine proper (Fig. 10). The esophagus lies dorsal and partly lateral to the pharynx.

Outside the cuticula layer of the esophagus occurs a layer of circular muscles covered in turn by a thin coat of longitudinal muscles. The circular muscles are more prominent in the region where the esophagus joins the intestine, and serve here as a sphincter muscle usually giving rise to a slight constriction in this region. Usually at about the level of the middle of the pharynx the esophageal stems on each side open into the ceca of the intestine proper. The internal cuticular layer of the esophagus ends abruptly at this point (Fig. 10). The intestinal ceca continue forward for a short distance, then bend abruptly and lead posteriorly.

The intestine shows no special regions. The two branches stretch nearly to the posterior tip of the body. They spread apart in the region of the ventral sucker, but approach each other closely immediately posterior to the sucker. They are also forced somewhat laterally by the ovary and testes. Just behind the posterior testis they again approach each other slightly. As in other related trematodes (*Azygia* and *Leuceruthrus*), the ceca are thrown into small folds throughout their length, the folds being more pronounced the higher the degree of body contraction. Each branch of the intestine ends blindly. There may be a slight difference in their length. That no significance can be attached to the frequently unequal length of the ceca is shown by the fact that the right is sometimes longer and sometimes shorter than the left.

The intestine is lined internally by a layer of cuboid or low cylindrical cells from which long wavy protoplasmic processes stream out into the lumen usually nearly filling it (Fig. 10). The internal boundary of these intestinal cells is very indefinite. The size of the cells is the same in very

small specimens and in the largest. A thin membrane surrounds the intestine which is also provided with a thin circular (internal) and longitudinal (external) muscle layers.

The excretory system is like that of similar forms. It consists posteriorly of a large single median tube which may be much swollen, lying between the branches of the intestine, and opening by means of a short duct at the posterior tip of the body. This tube branches a short distance behind the posterior testis, its two branches crossing the intestinal ceca ventrally and proceeding anteriorly lateral to these ceca. The two branches are continuous anterior to the oral sucker. The main excretory system consists then, of a Y-shaped tube with the two forks of the Y continuous. This tube may be thrown into folds comparable with those described for the intestine. Its outline in cross-section is very irregular and it can be seen to be continually receiving minute lateral branches. Its thin membranous lining is obscured by many deeply staining spherical granules which thickly adhere to the wall of the main tube throughout its length. These concretions are generally considered as waste products, and are commonly known in many trematodes.

Flame cells are numerous. They are small cells oval in shape, with prominent nuclei. Favorable sections show that they occupy ends of minute excretory ducts and that their tips are prolonged into a tuft of cilia about equal to the cell body in length. The cells measure about 14 by 8 $\mu$ .

The genital pore is ventral, median, between the two suckers and much closer to the oral sucker. It leads into a roomy genital atrium within which usually projects the nipple-shaped genital cone or papilla (Fig. 5). Both the genital atrium and the papilla are lined with cuticula which, however, becomes very thin at the tip of the cone. Just beneath this cuticula the wall of the atrium is strengthened by a thick layer of circular muscles. These muscles continue about the base of the papilla but gradually disappear toward its tip. Outside these circular muscles is a layer of longitudinal muscles, that is, muscles running in the direction of the long axis of the papilla. These muscles are continuous from the wall of the atrium into the papilla where they are internal to the circular muscles. Oblique muscles run off from the region of the longitudinal muscle layer of the atrium. In the solid-appearing tissue of the cone occur numerous nuclei which are more numerous near the tip of the papilla.

What at first appeared to be a marked difference in the size and occurrence of this papilla in the two species of *Otodistomum* led to a study of the permanency and variability of this organ. In the related genus *Azygia*, the genital atrium is usually without a papilla, the common sex duct opening at its base. This base of the atrium is, however, protrusible so that it can be thrust out papilla-like. Thus, here the genital papilla is only a momentary or temporary structure. Odhner (1911b: 518) says in

regard to this condition; "Dies konnte den Verdacht erwecken, dass es sich bei *Otodistomum* am Ende in derselben Weise verhielte; doch scheint mir dort die Papille einen mehr 'soliden' Eindruck zu machen."

Sections through *O. veliporum* from the Pacific showed the genital papilla almost always entirely absent or quite rudimentary in size. In *O. cestoides* the papilla was usually of robust form filling most of the atrium, or even entirely protruded from it (Fig. 6). In the latter case, the atrium itself is practically eliminated. In order to determine the constancy of the papilla, specimens of various sizes and degrees of body contraction were sectioned. Specimens collected in different years and killed in different solutions were also compared. The usual and contrasting conditions found are represented in Fig. 8 (*O. cestoides*) and Fig. 7 (*O. veliporum*). Of the specimens of *O. veliporum* sectioned, six showed the papilla absent, or a condition as in *Azygia*, three showed a small papilla (Fig. 7), while one showed a prominent papilla partially protruded from the pore (Fig. 29). Among eight specimens of *O. cestoides* sectioned, one showed the papilla entirely protruded (Fig. 6), six showed a robust papilla largely filling the genital atrium (Figs. 5 and 8), while one showed the papilla entirely absent (Fig. 28). Odhner's suspicion is therefore correct. Although the genital papilla has always been described and figured as a prominent feature in *Otodistomum* species it is capable of being entirely withdrawn as is normally the condition in *Azygia*. What appeared, then, to be a clear distinction between the two forms studied becomes a weak taxonomic character since it is variable and inconstant.

The atrium in *O. veliporum* from the Pacific almost constantly led very sharply posteriad and only slightly dorsad, while in the Atlantic form (*O. cestoides*) the slope of the atrium was almost directly dorsad and only slightly posteriad. This degree of slope of the atrium is probably associated with the condition of the papilla as when this structure was completely withdrawn in *O. cestoides* the atrium led sharply posteriad (Fig. 28).

Measurements on the size of the atrium and papilla in different specimens are as follows:

*Otodistomum veliporum*

Genital atrium		Genital cone	
1.	0.845    0.093 mm.	0.102	by 0.08 mm.
2.	0.9    by 0.06	0.075	0.035
3.	0.935    0.112		absent
4.	0.935    0.168	0.056	0.093
5.	0.935    0.149		absent
6.	2.04    0.32		absent
7.	1.57    0.3		absent
8.	1.57    0.28		absent
9.	1.25    0.23		absent
10.	0.9    0.5	1.25	0.43

*Otodistomum cestoides*

Genital atrium			Genital cone		
1.	0.243	× 0.187 mm.	0.168	×	0.149 mm.
2.	absent		0.71		0.52
3.	0.33	0.28	0.28		0.2
4.	0.617	0.355	0.317		0.317
5.	0.37	0.187	0.187		0.187
6.	0.6	0.6	0.39		0.54
7.	0.94	0.62	0.39		0.54
8.	1.25	0.15	absent		

It is certain that the size of the papilla is independent of general body contraction. Measurements No. 4 in the above table represent a strongly contracted specimen of *O. veliporum* and an extended specimen of *O. cestoides*. The size of this structure is also independent of the killing fluid. Sometimes the body wall projects lip-like about the genital pore. This condition also is not associated with the size of the papilla. A definite system of muscles about the papilla and in the neck region seems to be responsible for the protrusion and withdrawal of the papilla.

The exact mechanism for the protruding of the papilla is difficult to determine and probably depends upon a rather complex system of muscles. The longitudinal muscles about the wall of the atrium have processes which attach themselves to the anterior (or ventral) part of the atrium (Fig. 28). At the other end these muscles are continuous with the longitudinal body muscles. Contraction of these muscles of the atrium would have a tendency to widen and to pull forward the anterior part of the atrium. The actual pushing out of the base of the atrium to form the papilla is probably brought about by the numerous diagonal and dorso-ventral muscles of the neck region. Contraction of these muscles causing a compression of body tissue in that region would provide a pushing force at the base of the atrium. Once the movement of the extrusion has started, it would be aided by the contraction of the circular muscles in the wall of the atrium and base of the papilla. Of the two specimens with papilla protruded *O. cestoides* showed the ejaculatory duct somewhat coiled even in the papilla itself, while this duct was straight in the papilla of *O. veliporum*. The duct is always coiled between the cirrus sac and the papilla, and in unprotruded papillae. The sudden projection of sperm and seminal fluids through this muscular duct would have a tendency to straighten its coiled condition just as such an effect is brought about by sudden pressure of water in a coiled hose. This influence is, of course, an uncertain one in this case and even if present would probably have a negligible effect in elongating the papilla. The retraction of the papilla doubtless results from the contraction of the longitudinal muscles which it possesses.

The papilla probably functions as a copulatory organ. In the specimen of *O. veliporum* with protruded papilla (Fig. 29), a large mass of sperma-

tozoa was emerging from the genital duct at the tip of the papilla. Spermatozoa were also found crowding the distal tip of the vagina for a short distance, as well as in the genital atrium outside the papilla. None were found in the vagina posterior to the papilla. Eggs were frequently found in the atrium but only when the papilla was completely withdrawn, a fact which indicates that egg laying occurs while the papilla is completely subsided.

The two testes lie one immediately behind the other in the median line at about the center of the body. They are close together and very commonly are in contact with each other. This condition depends, however, upon the state of body contraction. The posterior testis is always slightly larger than the anterior testis. Each testis is surrounded by a fibrous-like membrane containing a few flattened nuclei. In adult forms from the Atlantic collection (*O. cestoides*) the size of the anterior testis was 0.62 to 1.25 mm. by 0.8 to 1.12 mm., while the posterior testis measured 0.8 to 1.37 mm. by 0.8 to 1.2 mm. The organs seemed to be rather consistently somewhat larger in *O. veliporum*.

The duct from the anterior testis leads from the ventral side of that organ near its anterior end, and extends anteriorly in the right half of the body. The other male duct leads from the ventral side of the posterior testis about  $1/4$  the length of the organ from its anterior end. Thus, in the specimen studied, the posterior testis measured 1.235 mm. and the duct opened 0.365 mm. from the anterior end. This condition may be at least partially due to the angle at which the sections were cut. The duct from the posterior testis leads anteriorly in the left half of the body. Both ducts at first lie ventral to the uterus but like the uterus pass dorsal to the ventral sucker, and in this region they also gradually become dorsal to the uterus. Slightly anterior to the posterior margin of the cirrus sac both ducts swing ventrally. The two do not unite until just before they empty into the seminal vesicle. Relations of the ducts were found to be the same in both *O. cestoides* and *O. veliporum*. Mühl Schlag, however, gives the ducts as arising from the median anterior borders of the testes and uniting into a common duct dorsal to the cirrus sac. The diameter of the vas deferens varies but when expanded measures 26 to 39 $\mu$  with a very thin membranous wall except in regions where the wall expands into prominent cells. (Fig. 25.)

The cirrus sac is large and elongate-ovoid in shape. It lies between the two suckers somewhat nearer the oral. In average sized specimens (23 to 35 mm.) it measures 0.84 to 1.02 mm. by 0.65 to 0.84 mm. It may attain a length of 1.3 mm. It is somewhat larger in *O. veliporum* where it reaches a length of 1.4 mm. The sac is definitely bounded by a thin membrane about which is an inconspicuous coat of circular muscles. Both seminal vesicle and prostate gland are contained entirely within the sac.

The seminal vesicle is a large swollen tube almost filling the posterior half of the cirrus sac. It is somewhat curved in shape and always packed with sperm cells. The sperm cells are thread-like in form with minute round heads. The wall of the vesicle is made up of flattened cells with large nuclei. The pars prostatica of the male duct leads from the anterior end of the seminal vesicle, proceeds posteriorly and dorsally, then bends anteriorly and runs diagonally forward to the anterior end of the cirrus sac. It is surrounded by the large prostate gland which fills the remainder of the cirrus sac. Just before the duct leaves the cirrus sac its character changes very abruptly into that of the ejaculatory duct.

The ejaculatory duct follows a much winding course leading to the tip of the genital papilla. Distally, it is joined ventrally by the vagina. The coiling of the duct in *O. cestoides* continues in the genital cone itself even when the latter is fully extended. The duct is lined by a thick layer of cuticula-like material continuous with the body cuticula. This layer attains a thickness of 10 to 13 $\mu$  and shows a folded irregular outline in cross-section. It is surrounded by a thick coat of circular muscles which becomes 20 to 25 $\mu$  in thickness near the cirrus sac. No longitudinal muscles could be noted.

In development the male reproductive system precedes that of the female. The seminal vesicle is filled with sperm cells some time before eggs appear in the uterus and before the vitellaria appear at all.

The ovary lies immediately in front of the anterior testis and usually in contact with it. In both organs the surface of contact is somewhat flattened. The ovary is therefore flattened on its posterior surface and its longest dimension is in the right and left direction. It may lie a little to one side of the testis, either to the right or to the left. (Figs. 13 to 18.) Its position in this respect is very inconstant and the various descriptions of the position of the ovary in this and similar forms is probably without significance. It is normally almost directly in front of the anterior testis. The size of the ovary in fully mature forms is 0.43 to 0.6 mm. by 0.78 to 0.9 mm. It is slightly larger in *O. veliporum* where it reaches 0.8 by 1 mm.

The ootype lies immediately anterior and slightly dorsal to the ovary with which it is in close contact. Both organs are surrounded by a common fibrous tissue which also separates the two. The ootype is somewhat smaller than the ovary. In an average sized specimen where the ovary measured 0.5 by 0.84 mm., the ootype measured 0.35 by 0.53 mm.

The oviduct leads from the middle anterior aspect of the ovary. It projects into the ovary in the form of a funnel-like structure with thick walls. This condition was found in both species (Fig. 11). The walls are composed of fibrous tissue which is continuous with the tissue covering the ovary and the ootype. This tissue is quite thick between ovary and ootype, and in it occur the two lateral vitelline ducts. As these ducts

approach each other they also tend to encroach upon the ootype so that they give the impression of pushing into it from the rear. Since the fibrous lining tissue becomes very thin between the yolk duct and the cells of the ootype, it is difficult to determine the exact point of penetration of the ootype by the yolk duct on either side. Frontal sections of *O. cestoides* indicate that the lateral ducts may penetrate the ootype before uniting to form the common yolk duct. More commonly, however, the two lateral ducts unite while still within the fibrous tissue close to the ootype and only the common duct actually penetrates into that organ.

Almost immediately after entering the ootype proper the oviduct is joined by the common vitelline duct and by Laurer's canal. The common vitelline duct is very short. A rather unusual condition was found in at least two cases where Laurer's canal instead of joining the oviduct opened at the point of union of the two yolk ducts, so that the three canals opened together into the oviduct (Fig. 24). In other cases noted, Laurer's canal was slightly to the right and appeared to join the right vitelline duct. Again, Laurer's canal may join the oviduct at about the same point as does the common yolk duct.

Laurer's canal is very well developed. It is lined with cuticula 4 to 6 $\mu$  in thickness. In medium-sized specimens the duct is about 25 $\mu$  in diameter. A circular layer of muscles surrounds it but no special longitudinal muscles could be made out. The tube is much coiled and leads dorsally and either anteriorly or posteriorly as will be shown later. Within the lumen of the canal are many sperm cells. In some cases, in the region adjacent the oviduct a few yolk cells were noted. A seminal receptacle is absent.

After receiving the yolk duct and Laurer's canal, the oviduct, now the uterus, becomes a small tube only about 26 $\mu$  in diameter with a thick wall made up of very definite cells with large nuclei. Into the lumen of this tube project cilia-like processes. The tube very shortly enlarges and the nature of its wall becomes one of large cuboidal and heavily granular cells (13 to 23 $\mu$  in thickness). This part of the tube coils about more or less within the ootype for a short time and continues also outside of that organ.

All stages in formation of the egg shell can be traced from the point where the yolk duct joins the oviduct. The shell material can be first seen as a shapeless irregular mass surrounding an egg cell and a group of yolk cells. Within the cellular-walled uterus region the eggs still lack their characteristic shape. The inner surface of the forming shell often shows vacuole-like spaces (Fig. 26). The cellular region of the uterus as it coils anteriorly soon passes over into a region characterized by a thin simple membranous wall. By the time the eggs have reached this region they possess hardened and fully formed shells.

The uterus contains thousands of eggs and extends anteriorly in many transverse coils. It passes dorsal to the ventral sucker and ventral to the



seminal vesicle. At about the level of the ventral sucker it becomes less coiled and the nature of its wall changes to produce a region which may be called the vagina.

The vagina like the male ejaculatory duct is lined internally by cuticula. It possesses two layers of conspicuous muscles, an inner circular layer and an outer longitudinal layer. The vagina contains few eggs and above the ventral sucker is almost a straight tube. It leads to near the tip of the genital cone where it unites with the male ejaculatory duct. There is a common duct for a distance of about  $25\mu$ .

In development the uterus first appears as a solid string of cells without a lumen. Sections of a very young specimen seem to show a lumen appearing first within the ootype the start of which appears early with the beginning of the ovary. It is an interesting fact that in slightly older specimens when the uterus can first be made out in toto-mounts but before eggs are being produced, this string-like beginning of the uterus assumes the coiling which characterizes the organ when filled with eggs. It winds transversely back and forth between the ovary and ventral sucker, crossing the body as many as 40 to 50 times, approximately the same degree of folding that is found in the adult.

The first eggs to be produced are abortive. A specimen 11.5 mm. in length showed the earliest egg still in the region of the ventral sucker. The most anterior eggs (15 to 20) were only about half the size of the others and were almost spherical with very thin shells. They measured from  $22.8$  to about  $30\mu$ , the smallest being most anterior. The eggs nearer the ovary were larger but still showed a very thin shell, in striking contrast to the thick shell found in the adult egg. No eggs in this specimen measured over  $68\mu$ , a measurement slightly below the average adult size.

The vitellaria are interesting because of the variation of their extent and arrangement. They are of the follicular type and consist of separate spherical bodies grouped in two longitudinal rows along the sides of the body. The follicles lie mostly ventral to the digestive system. They do not appear until relatively late in development, or just before eggs begin to be formed. At this time the follicles are very small, approximately the size of the eggs (about  $50\mu$  in diameter), but in the adult they reach a diameter of  $150$  to  $190\mu$ . Several hundred of these follicles are connected by ducts which unite into a common lateral duct on each side at the level of the ootype, and these two lateral ducts unite in the ootype as described. The rows of follicles are usually narrow, but the width of the rows often increases to such an extent that the two approach each other medianly. Thus, Miss Lebour (1908) figures the vitellaria massed together posterior to the testes. Such variations are not common, however, the two rows being usually distinctly separate. Irregular breaks or spaces free of follicles are common, and certainly can have no specific significance within the

genus *Otodistomum*. Even the differences in the vitellaria given by Odhner (1911b) to distinguish *O. cestoides* from *O. veliporum* are quite useless. He gives the vitellaria in *O. veliporum* as beginning behind the middle of the uterus and as being compressed into narrow rows, while in

TABLE 3  
VARIATION IN POSTERIOR EXTENT OF VITELLARIA IN *O. cestoides*

Body length <i>a</i>	Distance from posterior testis to posterior tip <i>b</i>	Extent of right vitellaria beyond posterior testis <i>c</i>	Extent of left vitellaria beyond posterior testis <i>d</i>	$\frac{b}{c}$	$\frac{b}{d}$
31. mm.	16. mm.	6.4 mm.	7.6 mm.	2.5	2.1
38.	21.	12.8	13.2	1.6	1.5
24.5	13.5	crosses over to left side	7.9	1.7	1.7
20.	8.3	8.3	7.3	1.	1.1
28.	13.5	10.6	9.8	1.2	1.3
17.	7.5	5.6	6.25	1.3	1.2
19.	9.	4.8	3.7	1.8	2.4
29.	14.	both unite in center	8.4	1.6	1.6
38.	18.	9.3	12.1	1.9	1.4
16.	8.	4.6	4.6	1.7	1.7
18.	8.	5.5	7.1	1.4	1.1
16.	6.	both unite in center	5.	1.2	1.2
11.	5.3	2.9	2.9	1.8	1.8
10.5	5.	2.4	3.1	2.1	1.6
10.8	5.	3.3	3.	1.5	1.6
10.5	5.	3.7	3.7	1.3	1.3
11.5	6.	3.9	3.9	1.5	1.5
11.	5.3	2.5	2.5	2.1	2.1
26.	10.5	7.4	7.2	1.4	1.4
26.	14.	united for 2.8 mm.	8.7	1.6	1.6
28.	15.	6.	6.	2.5	2.5
31.	17.	unites with left	7.4	2.2	2.2
28.	13.	unites with left	8.7	1.5	1.5
28.	15.	6.	6.	2.5	2.5
29.	15.	9.4	9.4	1.5	1.5
32.	16.	8.2	10.7	1.9	1.5

*O. cestoides* the follicles ordinarily begin in front of the middle of the uterus and are not as compressed. This distinction cannot be maintained. In *O. cestoides*, while the vitellaria have their anterior limit between the ovary and ventral sucker, approximately half way between these two organs, they may extend clearly beyond this mid-uterine point or may fail to reach it by some distance.

Posteriorly, the vitellaria always extend considerably beyond the posterior testis and practically always reach at least half the distance

between the hind testis and the posterior end of the body. Two cases (one in *O. veliporum* and one in *O. cestoides*) were noted wherein the vitellaria extended to the extreme posterior tip of the body. One row of the follicles may be several millimeters longer than the other. The rows may unite and run together for several millimeters either medianly or on one side. As such variation in these organs is unusual a table has been prepared to show more detailed measurements (Table 3).

The average egg size for *O. cestoides* was 69.4 by 46.2 $\mu$  as derived from over 50 measurements. This size agrees with data by Odhner (1911b) who gives 0.065 to 0.072 by 0.043 mm., and Cooper (1915) who gives 0.070 by 0.042 mm. The thickness of the egg shell measured under oil immersion lens averaged about 4.5 $\mu$ . This thickness is somewhat above the measurements of Odhner, who gives 0.003 mm. and Cooper, who gives 0.0028 mm. The eggs of *O. veliporum* averaged 85.5 by 57.8 $\mu$ .

## GROWTH CHANGES IN *OTODISTOMUM CESTOIDES* WITHIN THE FINAL HOST

Since it is clear that the trematodes must be slightly under 2 mm. in length when first entering the skate, there is a growth within that host to about 40 times. Moreover, the parasite increases its size by six or seven times after it has become sexually mature. This growth of the worm within the skate is marked not only by degree, but also by a regional localization, which results in very different conditions of body proportions in the young and in the adult. The growth is largely in the region posterior to the ventral sucker, and consists mostly in body elongation.

A study was made of this localized growth and its effects upon various body proportions. The material at hand was especially favorable for such study not only because the extremes in size were conspicuous, but also because all intermediate sizes were available.

Regional growth in trematodes has been noted in a general way by various workers. Braun (1894:567) says of trematodes in general: "— junge Exemplare sind nicht nur absolut, sondern auch relativ kürzer, indem besonders das hintere Körperteil mit der Entwicklung der Geschlechtsorgane bedeutend an Länge zunehmen kann. Gleichzeitig treten auch andere Veränderungen der Gestalt auf, die so bedeutend sind, dass es oft der Uebergangsstadien bedarf, um eine Jugendform zu diagnosticiren."

As early as 1870 van Beneden stated that the young form of *Dist. hispidum* was entirely different from the adult.

A proportionally greater increase in length than in width was indicated by von Linstow (1890) for *Dist. cylindraceum*, but only a few forms were measured. Specimens measured were 4.5 by 1.4 mm., 6–7 by 1.5 mm., and 13 by 2 mm.

The liver fluke (*F. hepatica*) shows a very marked increase of the posterior regions at the time of sexual maturity as shown by both Thomas (1883) and Leuckart (1886). This growth change also affects the ventral sucker which increases its size ratio to the oral sucker. Thus, according to Thomas (1883:132) the suckers are of nearly equal size in the cercaria while in the adult the diameters of the oral and the ventral suckers have the ratio 1 : 1.35. In *F. hepatica* the body form also increases rapidly in width.

Barlow (1923) gives measurements of hundreds of individuals of *Fasciolopsis buski*. While the size changes in this form are interesting, there does not appear to be conspicuous changes in proportions.

Cort (1921) has given the changes in body proportions with growth in *Schistosoma japonicum*. It is interesting that these changes parallel very closely the changes in *O. cestoides*, an entirely unrelated form. Like the fish trematode, the adult blood fluke is elongate, whereas the young are short and wide. The adult *Schistosoma japonicum* may increase its size as many as 100 times over that of the cercaria. The changes "consist in a very great increase of the length in ratio to the width, an enormous increase of the post-acetabular region of the body as compared with the pre-acetabular, and a gradual assumption of the secondary sexual characteristics which produce the sexual dimorphism of the adult." Especially interesting are changes in the size ratio between the two suckers. "In the cercaria the ventral sucker is only about  $\frac{1}{3}$  the diameter of the oral sucker. In an early stage of development, the suckers become about equal in size, and in later stages the ventral sucker is constantly larger than the oral sucker." This progressive change in sucker ratio is to be contrasted with the constancy of this ratio in *O. cestoides* as will be shown later.

Growth phenomena have been noticed in the *Azygia* group by Ward (1910) for *A. sebago* and by Mühlschlag (1914) for *Otodistomum veliporum*. Ward says (of *A. sebago*): "The anterior region assumes the form of an ellipse surrounding the two suckers. This region changes relatively little in size with growth. In one of the smallest specimens (measuring 1.6 mm.) the distance between the centers of the two suckers was 0.5 mm. In one 10 mm. long, this distance measured 1 mm." Mühlschlag found by measuring the largest and smallest specimen of his collection of *Otodistomum veliporum* that the neck region compared with the body region was 1 : 4 in the young forms and 1 : 7.8 in the largest individual. He concludes: "dass bei verschiedener Grösse der Tiere der Hinterkörper relativ stärker wächst als der Vorderkörper."

In *Otodistomum cestoides* the contrast in form between a very young and a sexually mature individual can be seen by comparing Fig. 1 and Fig. 2. Measurements were made on over 200 specimens varying in size from 2.3 mm. to 65 mm. The measurements (taken on alcoholic specimens) included length, width at broadest point, and distance from anterior end to the posterior margin of the opening of the ventral sucker. The margin of the opening was chosen because the outline of the ventral sucker itself is usually not distinct in unmounted specimens. The position of the opening varies somewhat in relation to the outline of the sucker, but, in general, approximates very constantly the true position of the sucker. All measurements can be considered only as approximate as most were taken with a millimeter rule which necessitated estimations of half and quarter millimeters. The smaller specimens were measured microscopically.

The youngest specimens (which very probably represent the earliest condition in the skate) are strikingly unlike the adult in body proportions.

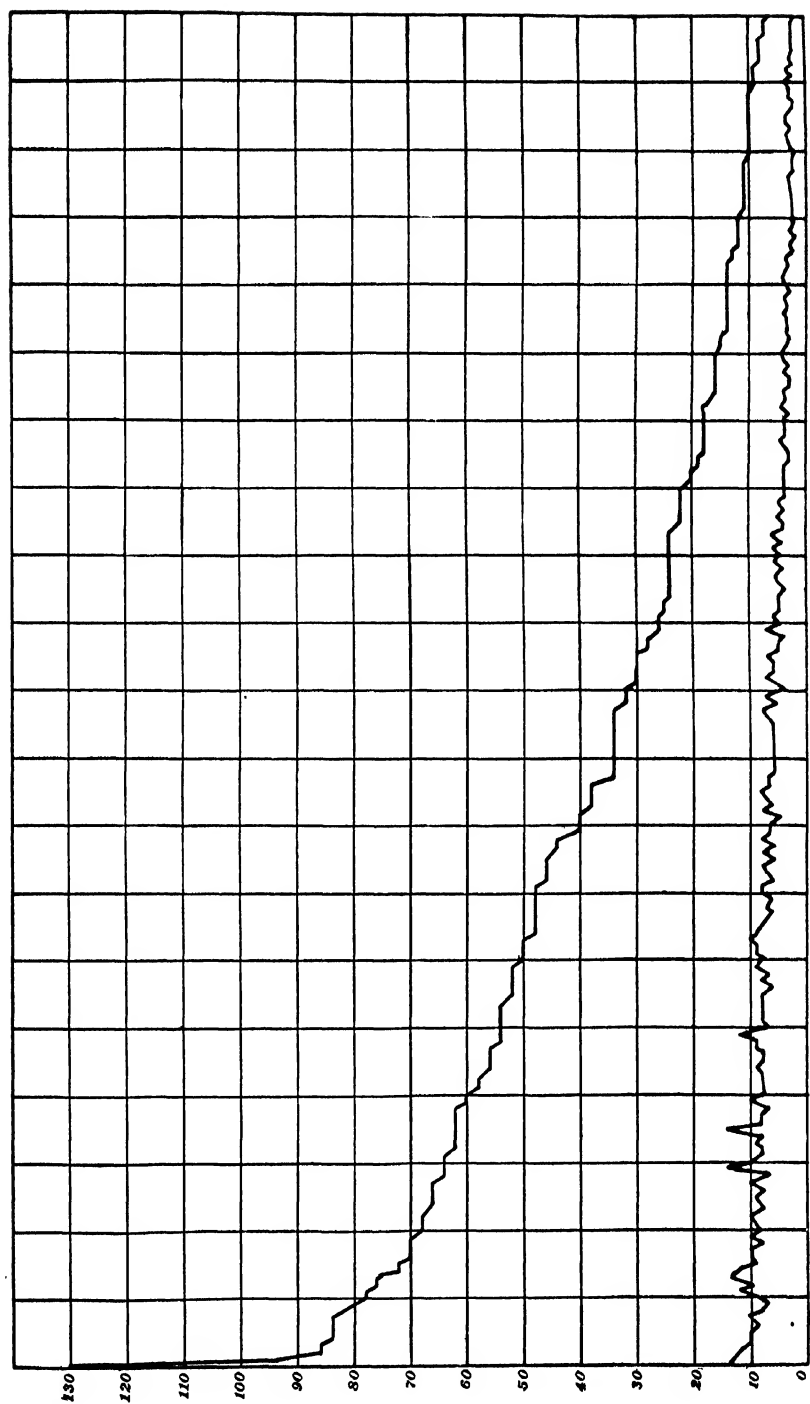


CHART 1. Graphic representation of proportions between total body length and distance from ventral sucker to anterior end in 200 specimens of *Oslodistomum cestoides*.

The base line (0) represents the anterior ends, the upper curve posterior ends of specimens. The lower curve indicates the positions of the ventral suckers. Ten individuals are represented between successive vertical lines. The horizontal lines indicate half-millimeters in multiples

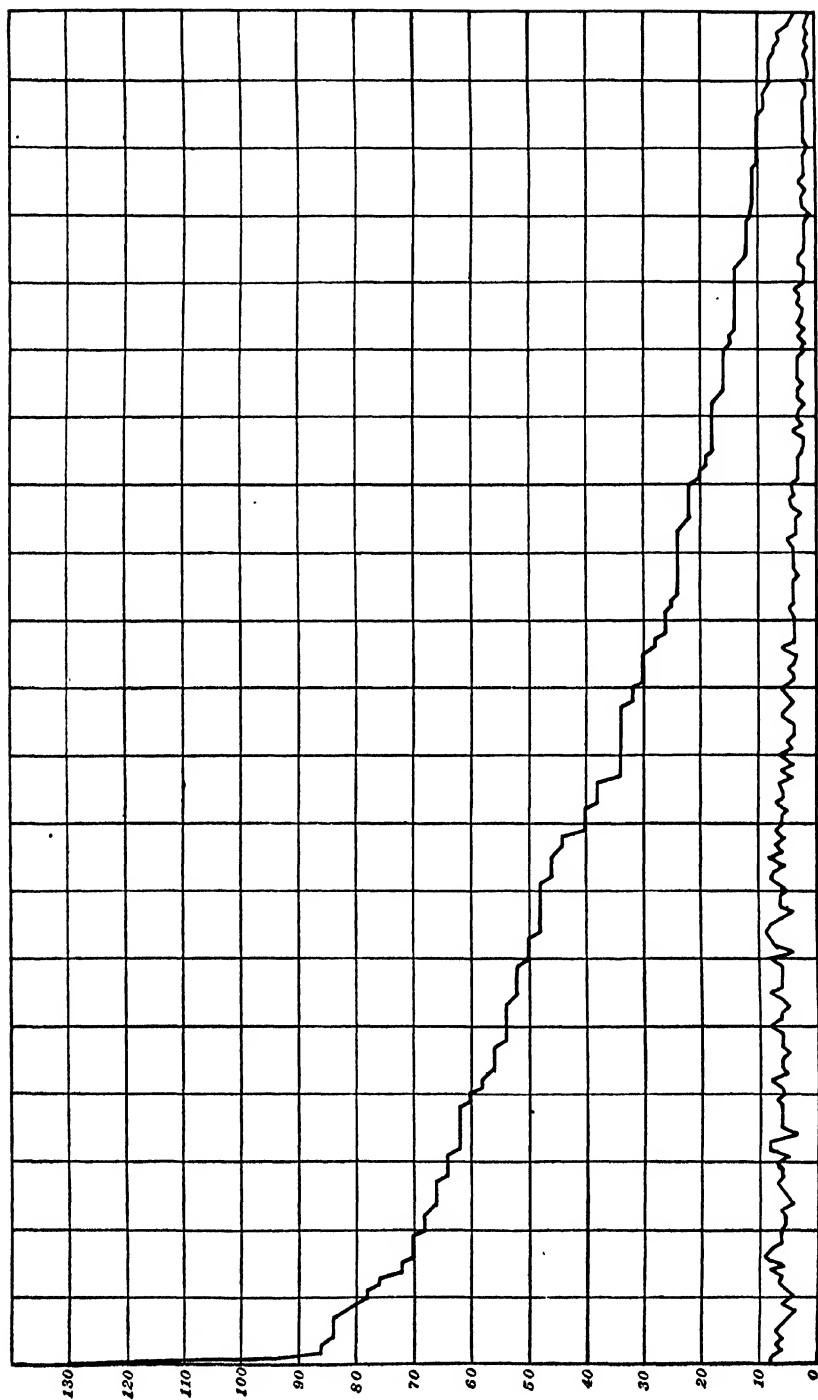


CHART 2. Graphic representation of proportions between total body length and body width in 200 specimens of *Ostodistomum cestoides*. The base line (0) represents the anterior ends, the upper curve the posterior ends of specimens. The widths of corresponding specimens are represented by the lower curve. Ten individuals are represented between successive vertical lines. The horizontal lines indicate half-millimeters

Thus, in individuals 2 or 3 mm. in length the ventral sucker is located just anterior to the center of the body, the proportion of the region in advance of the posterior border of the sucker to the entire body length being 1 : 2.3, 1 : 2.5, 1 : 3, etc. (see Chart 1). As the trematodes increase in size, the region posterior to the ventral sucker gradually and constantly gains in size in proportion to the anterior region, which grows relatively little. This change can be followed in the accompanying chart (Chart 1) on which the body lengths and positions of the ventral suckers have been plotted. The total length in half millimeters is plotted on the vertical lines as is also the position of the ventral sucker. Each vertical line, then, represents one trematode so that if the base line be considered as the anterior ends of the worms, the points where the lower curve intersects the vertical lines represent the positions of the ventral suckers, while the upper curve represents the posterior ends of the trematodes. Ten specimens are represented between two successive vertical lines. The change in proportion and the constancy of the change can be seen at a glance.

The fluctuations in the lower curve are due to differences in contraction of individual specimens. Because of such differences the chart can only be considered as approximate. Quite a number of the specimens were stretched slightly by hand when killed in order to prevent contraction. Separate tables and charts were prepared, however, for individuals not so treated, and in every case results were the same as in the complete table of all individuals. In the collection of material numerous of the more mature trematodes were destroyed for the purpose of obtaining eggs. Without doubt, the only change which would be caused in the chart by such loss would be to reduce the degree of incline or steepness of the upper curve in the region above horizontal line 50 or 60.

Study of the data on length and width of the trematode at different stages showed corresponding results. The measurements are plotted in Chart 2 where it can be seen that increase in width is very little in comparison with increase in length. The elongate form which gives the adult worm a cestode-like appearance is only gradually assumed with age, and the youngest individuals are very characteristically trematode-shaped. In Chart 2 the distance on any vertical line from the point of intersection of the lower curve to the base line represents the width of an individual specimen whose length is represented by the distance from the *upper* curve to the base line. As the specimens are arranged in order of length, here again all fluctuations due to varying degrees of contraction appear in the lower curve only.

In spite of these radical changes in body proportions, the ratio between the sizes of the two suckers remains constant. That is, the two suckers grow equally evenly, although the body is growing much more rapidly posteriorly.



This constancy of the sucker ratio is somewhat unexpected since other trematodes, especially when body proportions are altered, show an increase of the ventral sucker over the oral. Most conspicuous is the actual reversal in sucker proportion in *Schistosoma japonicum* where, as already given, the ventral sucker is smaller than the oral in the cercaria, but later assumes equality with it, and in the adult is definitely larger. A similar tendency in *F. hepatica* has also been noted.

The following table (Table 4, Column *b/c*) shows very clearly how all sizes of *O. cestoides* vary closely about the average ratio (oral sucker .66 of the ventral sucker). It is true that in the four smallest specimens is found the largest ratio (up to 0.82), but specimens almost as small show a ratio slightly below (0.64 and 0.65) the average, and some of the largest individuals show a ratio of 0.7 or more.

TABLE 4  
SUCKER SIZE IN RELATION TO GROWTH IN *O. cestoides*

Body length	Body width	Diameter of anterior sucker	Diameter of ventral sucker	$\frac{b}{c}$	$\frac{c}{a}$
(a)		(b)	(c)		
39. mm.	2.87 mm.	1.43 mm.	2.18 mm.	.65	17.8
38.	2.06	1.25	1.81	.7	21.
38.	2.25	1.312	2.	.66	19.
32.	2.3	1.06	1.62	.65	19.
31.	3.5	1.56	2.18	.71	14.2
31.	2.3	1.3	1.8	.72	17.2
29.	2.75	1.43	2.31	.62	12.5
29.	2.3	1.	1.56	.63	18.5
28.	2.18	1.12	1.75	.64	16.
28.	1.3	1.37	2.	.68	14.
28.	2.18	1.	1.68	.58	16.6
28.	2.87	1.18	1.68	.7	16.6
26.	1.6	.93	1.37	.67	18.9
26.	1.87	1.06	1.37	.77	18.9
24.5	2.37	1.25	1.87	.61	13.
24.	2.8	1.37	2.18	.62	11.
21.	3.1	1.25	1.75	.75	12.
20.	1.68	0.878	1.327	.66	15.
19.	2.12	1.	1.437	.71	13.9
18.	2.5	1.14	1.77	.64	10.1
17.	2.5	1.028	1.77	.57	9.6
16.	2.06	0.916	1.34	.68	11.9
16.	2.5	1.02	1.53	.66	10.4
14.	1.9	1.06	1.5	.64	9.3
13.	2.1	1.5	1.5	.66	8.6
12.	1.8	1.	1.37	.73	8.7
11.5	2.1	0.93	1.5	.62	7.6
11.	1.5	0.75	1.12	.66	9.8
11.	2.1	0.93	1.5	.62	7.3

TABLE 4 (continued)

Body length	Body width	Diameter of anterior sucker	Diameter of ventral sucker	$\frac{b}{c}$	$\frac{c}{a}$
(a)		(b)	(c)		
10.8 mm.	1.75 mm.	0.75 mm.	1.25 mm.	.6	8.6
10.5	1.8	0.68	1.31	.52	8.
10.5	1.3	0.68	1.06	.64	9.9
6.5	1.	0.54	0.785	.68	8.3
6.06	1.12	0.525	0.748	.7	8.
5.	0.93	0.448	0.654	.67	7.6
4.5	0.56	0.448	0.654	.67	6.9
4.37	0.9	0.414	0.673	.62	6.5
4.31	1.047	0.504	0.766	.65	5.6
4.18	0.937	0.467	0.635	.73	6.5
4.125	0.991	0.397	0.617	.64	6.6
3.6	0.75	0.414	0.635	.65	5.6
2.37	0.562	0.317	0.43	.73	5.5
2.25	0.748	0.414	0.504	.82	4.2
2.18	0.71	0.355	0.43	.82	5.
1.9	0.56	0.28	0.39	.74	4.8
Average				.66	

Another interesting point is the relatively much larger size of the suckers in comparison with body size in the young. This observation would follow from the fact that the diameters of the suckers keep pace with the width of the worm. This marked change in proportion between sucker diameter and body length can be followed in Table 4, column  $c/a$ . In the smallest specimens, the body length was 4.8 times the diameter of the ventral sucker, while in all the largest specimens measured the body length was about 20 times the diameter of the ventral sucker. The change between these two extremes is seen to be consistent and gradual exactly as was the change body length and width. Young forms in general show the body length to be about 5 times the diameter of the ventral sucker, medium sized specimens have a length about 10–11 times this diameter, while a specimen 38 mm. long was 21 times longer than the diameter of the ventral sucker.

It is interesting to note what effect, if any, the arrival at sexual maturity has upon these growth rates. The uterus is located posterior to the ventral sucker, and it might be expected that the relatively sudden filling of the uterus with eggs would affect growth in this region. The body size at which the trematode attains sexual maturity is quite constant. Almost invariably eggs begin to be produced when the worm has a length of about 11 mm. A few eggs have been found in specimens 10.5 mm. in length. It can be stated quite certainly that sexual maturity is attained between the body lengths of 10 and 15 mm.

Reference to the charts shows 49 specimens between 5 and 10 mm. in length, 30 between 10 and 15 mm. in length, and 22 between 15 and 20 mm. in length. All specimens of these sizes were preserved. As fewer individuals were found intergrading between the sizes 10 and 15 mm. than between 5 and 10 mm., it might be inferred that growth is more rapid in the former case. The indication can only be considered as a slight one, however, as the difference is not large, the numbers are somewhat few, and there is a possibility of various unknown factors such as infection rate.

Further data on the effect of sexual maturity on growth can be obtained by comparing distances from the posterior testis to the ventral sucker (region of uterus) and from this same point to the posterior end of the worm (tail region). At a certain period (11 to 15 mm.) the uterus becomes quite suddenly crowded with eggs. Whether this change alters the proportions of the length of the uterus region to the length of the posterior region where no organs of importance are located, and where no important change is occurring, can be shown approximately by comparing the lengths of these regions in mature and immature specimens. In 21 wholly mature

TABLE 5

COMPARISON OF UTERUS REGION WITH POSTERIOR BODY REGIONS IN YOUNG SPECIMENS  
OF *Otodistomum cestoides*

Body length	Length of tail region (a)	Length of uterus region (b)	$\frac{b}{a}$
14. mm.	6.5 mm.	5. mm.	.7
13.	7.	3.56	.51
12.	6.	3.5	.58
11.5	5.3	3.	.56
11.	5.3	3.	.58
11.	5.25	2.37	.45
10.8	5.	3.25	.65
10.5	4.8	2.87	.6
10.5	5.	2.4	.58
10.	5.8	2.18	.37
6.5	3.25	1.43	.44
6.06	3.	1.47	.49
5.	2.3	1.12	.48
4.5	1.68	1.	.6
4.187	1.68	0.937	.55
4.37	1.5	1.	.66
4.31	1.5	0.75	.5
4.125	1.9	0.687	.35
3.6	1.7	0.57	.34
2.37	1.	0.525	.52
2.18	0.74	0.37	.5
Average			.493

individuals the length of the uterus region averaged 0.67 the length of the tail region. In 21 immature individuals including a few very young forms, this uterus region averaged 0.493 the length of the posterior region. That is, the uterus region upon becoming filled with eggs increases on the average its ratio to the tail region by about 0.2. While this increase is small, it is very definite. Reference to Tables 5 and 6 shows that the proportion of the

TABLE 6

COMPARISON OF UTERUS REGION WITH POSTERIOR BODY REGION IN ADULT SPECIMENS OF  
*Otodistomum cestoides*

Body length	Length of tail region	Length of uterus region	$\frac{b}{a}$
	(a)	(b)	
38. mm.	21. mm.	12.5 mm.	.6
38.	18.	14.	.77
32.	16.	11.	.67
31.	11.5	9.	.78
31.	17.	9.	.53
29.	14.	9.75	.69
29.	15.	8.5	.56
28.	14.	10.	.71
28.	15.	9.	.6
28.	18.	7.	.4
28.	12.5	10.	.8
26.	11.06	11.06	1.
26.	15.	8.	.56
24.5	13.2	7.1	.53
21.	12.5	6.25	.5
20.	8.	8.	1.
19.	10.	6.5	.65
18.	7.75	5.93	.7
17.	7.5	5.8	.78
16.	6.12	6.12	1.
16.	7.9	4.6	.58
Average			.67

uterus to the tail region in the young forms measured attained only once a point as high as 0.7 and went as low as 0.34. Moreover, even in these forms the uterus region tended to be slightly greater in individuals with a few eggs (those specimens 10 to 14 mm. in length). Of the mature forms, however, the uterus region was never less than 0.4 the tail region and several times attained equal length with it.

The increase of the length of the body posterior to the ventral sucker over the length anterior to this sucker is by no means due entirely, however, to this seeming increase in the uterus region. To show this fact, measurements of the neck region (that region from the anterior end to the ventral sucker) were compared with measurements of the tail region. The neck

region in 18 immature or recently mature forms averaged 0.77 the length of the tail region, while in 12 mature forms the neck region averaged only 0.39 of the tail region. That is, while the uterus region is gaining on the tail region the latter is also gaining even more rapidly on the neck region (Tables 7 and 8).

TABLE 7

COMPARISON OF NECK REGION WITH POSTERIOR BODY REGION IN YOUNG SPECIMENS OF  
*Otodistomum cestoides*

Body length	Anterior end to ventral sucker (a)	Posterior testis to posterior end (b)	$\frac{a}{b}$
13. mm.	3. mm.	7. mm.	.43
11.5	3.5	5.3	.66
11.	3.	5.3	.56
11.	3.	5.25	.57
10.8	2.56	5.	.51
10.5	2.68	4.8	.56
10.5	2.75	5.	.55
6.5	2.12	3.25	.65
6.06	1.5	3.	.5
5.	1.87	2.3	.81
4.5	1.8	1.6	1.1
4.187	1.8	1.68	1.05
4.37	1.87	1.5	1.24
4.31	1.37	1.5	.91
4.125	1.4	1.9	.74
3.6	1.25	1.7	.73
2.3	0.93	1.	.93
2.18	1.04	0.74	1.4
Average			.77

In stating that the uterus region increases its proportion to the tail region, it has been assumed that the position of the posterior testis is relatively stationary. If, however, the uterus, in filling with eggs, pushes the reproductive organs backward, then the increased growth in the uterus region is only apparent, since the position of the hind testis was taken as a point of measurement. Similarly, illusions would follow from any local movement of the gonads either forward or backward within the body. In general, the gonad group appears to occupy a fixed position. Commonly, especially in extended specimens, the two testes are separate from each other by a short space. When the two organs are in contact with each other the surface of contact becomes flattened. Thus, if the uterus did have a tendency to force the gonads backward, some leeway would be allowed this movement before it exerted an influence on the position of the hind testis, upon which present measurements were based.

TABLE 8

COMPARISON OF NECK REGION WITH POSTERIOR BODY REGION IN ADULT SPECIMENS OF  
*Otodistomum cestoides*

Body length	Anterior end to ventral sucker (a)	Posterior testis to posterior end (b)	$\frac{a}{b}$
38. mm.	5. mm.	21. mm.	.24
31.	6.	17.	.35
38.	6.	18.	.34
29.	5.	14.	.35
28.	4.	14.	.28
24.5	4.	13.2	.3
20.	4.	8.	.5
19.	3.5	10.	.35
18.	3.	7.75	.38
17.	4.	7.5	.53
16.	4.	6.12	.65
16.	3.5	7.9	.44
		Average	.39

Some slight evidence that the crowded uterus may cause a forcing back of the ovary against the anterior testis is found in certain variations in the relative position of the pore of Laurer's canal. This pore furnishes a fixed point and if it retains a constant position in relation to the ovary in young and in mature specimens, it can be inferred that the position of the ovary is also constant. Such a relation does not exist. The pore was found to be sometimes anterior to the anterior end of ovary, sometimes almost exactly dorsal to it, and sometimes slightly posterior to it. As serial sections were necessary to determine this point, it was ascertained in relatively few cases. In *O. cestoides* the pore was always found to be posterior to the anterior border of the ovary in young or recently mature specimens, and usually anterior to it in mature forms. One exception in both *O. cestoides* and *O. veliporum* shows that the pore may be posterior to the anterior edge of the ovary even in mature individuals. In all young forms measured the pore was posterior to this point. A table follows showing the position of the pore in specimens of different ages:

*O. cestoides*

Length	Maturity	Pore in relation to anterior end of ovary	Distance
10 mm.	uterus with few eggs	Posterior	0.56 mm.
Small	immature	"	0.18
Small	only a few eggs in uterus	"	0.23
14 mm.	Recently mature	Anterior	0.14
25 mm.	Mature	"	0.18
Large	Mature	"	0.18
Large	Mature	Posterior	Slight

*O. veliporum*

23 mm.	Mature	Anterior	0.6 mm.
25 mm.	Mature	Posterior	0.285

In any case, the extent of this shifting as far as it is indicated by relative pore position is not sufficient to affect materially the position of the hind testis. Conclusions in regard to growth changes can be more graphically expressed by means of a diagram (Diagram 1).

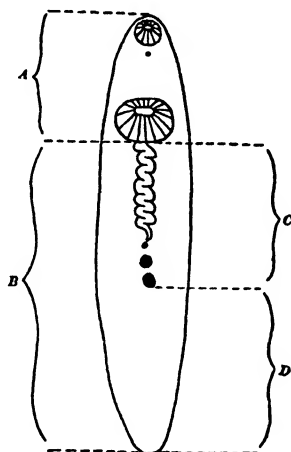


DIAGRAM. 1. Diagram to show growth changes in *Olodistomum cestoides*. Distance B constantly grows faster than Distance A, even before sexual maturity. Distance C increases slightly its proportion to D after sexual maturity. Distance D increases in length more rapidly than A, even after sexual maturity. Body length increases much more rapidly than body width. Size ratio of the two suckers does not change with size of the worm. Suckers are proportionally much larger in young.

### COMPARISON OF *OTODISTOMUM CESTOIDES* AND *O. VELIPORUM*

The close resemblance of these two species has already been noted. Odhner (1911b) gives the following differences:

<i>O. veliporum</i>	<i>O. cestoides</i>
1. Size: 50 mm. by 5 to 6 mm.	Size: to 65 mm. by 3 to 5 mm.
2. Ratio of suckers: 3 : 5	Ratio of suckers: 3 : 4
3. Vitellaria beginning behind the middle of uterus field, compressed into narrow bands.	Vitellaria usually beginning in front of middle of uterus field, not so narrowly compressed.
4. Egg: 0.86 by 0.06 to 0.063 mm.	Egg: 0.065 to 0.072 by 0.043 mm.
5. Thickness of egg shell 0.006 mm.	Thickness of egg shell 0.003 mm.

Of these differences, numbers 2 and 3 are certainly useless as all conditions involved were commonly found in the present studies of the single species, *O. cestoides*. Odhner placed importance on the thickness of the egg shell.

Mühlschlag (1914) worked on *O. veliporum* and concluded that the following features separate it from *O. cestoides*: (1) its body is less in length, greater in width; (2) its eggs are larger, and (3) have a much thicker shell. He found that the thickness of the egg shell of *O. veliporum* to reach  $7\mu$  or more than twice as thick as commonly reported for *O. cestoides*.

The trematode from *Raia binoculata* from the Pacific has already been frequently compared with *O. cestoides* from the Atlantic "barn-door" skate. It has been seen that the Pacific form presents very few significant differences. Chief among these differences is the egg size. The average egg size from over 50 measurements in the Pacific form gives 85.5 by  $57.8\mu$  as compared with 69.4 by  $46.2\mu$  in *O. cestoides*. This difference is real, constant, and significant. In no case did the egg size overlap between the two species. Thus, the eggs in the Pacific form agree almost exactly with the reported egg size for *O. veliporum*.

One of the other reported differences between these two species is a slightly greater body width in *O. veliporum*. The average width of 75 Atlantic specimens (*O. cestoides*) between 23 and 50 mm. in length was 3.22 mm. The average width of 65 Pacific specimens (*O. veliporum*) between the same length limits was 3.81 mm. Thus, again the Pacific form agrees with descriptions of *O. veliporum*. The Pacific specimens were quite constantly of greater thickness, however, and their slightly greater width might be due to an average higher degree of body contraction.

The only other specific criterion to be applied is the thickness of the egg shell. *O. veliporum* supposedly possesses a much thicker egg shell than



does *O. cestoides*. In this particular, the Pacific form studied does not agree with the published records for *O. veliporum*. An average of numerous measurements on the egg shell gave a thickness of about  $4\mu$ . For *O. cestoides* an egg shell thickness of about  $4.5\mu$  was found. Thus, instead of having an egg shell twice as thick as does *O. cestoides*, the Pacific form actually has a slightly thinner egg shell. Measurements were taken on mature eggs in distal regions of the uterus. The eggs nearer the ovary had a slightly thicker shell. Even though this discrepancy in egg shell thickness appears to be a constant feature in material studied, it hardly seems to be in itself a specific character. In the first place, the absolute difference in egg shell thickness between the Atlantic form and records for *O. veliporum* is slight (about  $2\mu$ ) since the Atlantic material showed an egg shell somewhat thicker than recorded for *O. cestoides*. Again, such minute measurements are difficult to determine exactly, especially as slightly oblique sections through the egg exaggerate the apparent thickness of its shell. Finally, the constancy of this feature is not well established, as is, for example, egg size in this genus.

In respect to other differences noted between the two forms, the condition of the genital atrium and papilla has already been discussed and showed to be unreliable as a specific character. It can only be said that, in general, the genital papilla was either absent or small in size in *O. veliporum*, and usually prominent and robust in *O. cestoides*. It may, however, be flattened out entirely in *O. cestoides* and entirely protruded in *O. veliporum*.

The genital organs seemed proportionally somewhat larger in *O. veliporum*. Actual measurements (in millimeters) on specimens of approximately similar size are as follows:

<i>O. cestoides</i>			<i>O. veliporum</i>		
Length			Length		
32 mm.	Testis (ant.)	0.9 by 0.87	32 mm.	Testis (ant.)	1.25 by 1.25
	" (post.)	1. 0.81		" (post.)	1.5 1.25
	Ovary	0.43 0.81		Ovary	1. 0.75
31	Testis (ant.)	0.68 by 0.9	30	Testis (ant.)	1. by 0.9
	" (post.)	0.8 0.9		" (post.)	1.27 1.
	Ovary	0.5 0.68		Ovary	0.8 1.
24	Testis (ant.)	0.89 by 0.37	25	Testis (ant.)	1. by 0.89
	" (post.)	0.78 0.86		" (post.)	1.3 0.89
	Ovary	0.46 0.7		Ovary	0.8 0.6

A 39 mm. specimen of *O. cestoides* agreed more nearly with the 32 mm. specimen of *O. veliporum* in gonad size, as follows:

39 mm.	Testis (ant.)	1.25 by 0.87 mm.
	Testis (post.)	1.37 0.9
	Ovary	0.6 0.9

These differences in gonad size are not, however, sufficient to be significant. Miss Lebour (1908) figures very large gonads for her species which was clearly *O. cestoides*.

From this study, it has been concluded that the Pacific material represents *Otodistomum veliporum*. Furthermore *O. veliporum* and *O. cestoides* are shown to be even more similar than has hitherto been pointed out. The most certain distinction is found in egg size. *Raia binoculata* (= *R. cooperi*) is a new host for *O. veliporum*.

*O. veliporum* (Creplin) has the following synonyms:

<i>Dist. veliporum</i> Creplin	
<i>Dist. insigne</i> Dies.	
<i>Dist. microcephalum</i> Baird	} according to Ariola 1899
<i>Dist. scymni</i> Risso	
<i>Fasc. squali grisei</i> Risso	
<i>Dist. veliporum</i> of Johnstone 1902	

It has been recorded from the following hosts: *Notidanus griseus*, *Notidanus cinereus*, *Echinorhinus spinosus*, *Carcharias milbertii*, *Raia batis*, *R. clavata*, *R. fullonica*, *R. radiata*, *R. lintea*, *R. binoculata*, *R. stabuliforis* (= *R. laevis*), *Scymnus nicaeensis*, *Acanthias vulgaris*, *Carcharias* sp., *Laemargus melanostoma*, *Scyllium canicula*, *Chimaera monstrosa*, *Carcharias rondeletti*, *Centralophus pompilus*.

THE MIRACIDIUM OF *OTODISTOMUM CESTOIDES*

[FIGS. 31-43]

The first larval form or miracidium of *O. cestoides* was studied from live material and in toto-mounts. As the larva is well developed and ready to hatch when the eggs are laid, sections of eggs in the vagina formed the basis for study from sections. Many thousands of the eggs can be obtained by cutting the adult worm just beneath the ventral sucker and pressing out the eggs in the distal portion of the uterus. This method gives a mixed culture of eggs of various degrees of maturity. A more uniformly mature collection results from saving only the eggs from the vagina region. Unsuccessful attempts were made to secure eggs that had been normally laid. Adults were kept both in sea-water and in sea-water with mucous and fragments from the stomach of the host. In the latter case, some specimens were kept alive two or three days, but in no case were any eggs obtained. There is no reason to believe, however, that the eggs in the vagina do not represent the normal condition of the eggs when laid.

The eggs can be readily hatched. They were kept in sea-water in vials surrounded by running sea-water. The water in the vials was changed twice daily. The eggs were found to be very hardy. In mixed cultures containing many immature egg stages, hatching larvae appeared most frequently only after 7 to 10 days. In the case of cultures of only the most mature eggs, several miracidia were observed only 5 hours after the eggs had been removed from the worm. This very early hatching shows that the larva is fully developed in the egg at the time of oviposition. In general, even when the eggs in a vial seemed quite uniform, no uniform period of hatching was observed. Only a small proportion of the eggs hatched, and these hatchings, few at a time, extended over periods of some days (up to 15). The large number of cultures undertaken gave ample opportunity of studying the rather peculiar miracidium.

The youngest immature eggs are pale yellow in color and quite transparent. They average only slightly smaller than mature eggs and the thickness of the shell seems to be about the same at all stages (in *O. cestoides*). In the early stages the embryo consists of only a few cells collected at the opercular end of the shell, while the rest of the space is occupied by numerous yolk cells. These latter gradually disappear as the embryo grows, until the egg shell seems to contain a uniform mass of cells.

The more mature eggs while alive have a characteristic appearance. The shell is brownish-yellow in color. A few small, globular bodies are

scattered about within the shell while at one end, the anterior, a dark opaque granulated area appears, concealing the anterior tip of the embryo. This area thins out posteriorly so that a dark crescent-shape appearance is given (Fig. 31). The same condition is described by Leuckart (1886:380) for *D. lanceolatum*. Just posterior to this area and within the body of the embryo are two conspicuous, hump-like structures continuous anteriorly, but of two parts (resembling lobes) posteriorly. What was probably a similar structure was seen and pictured by von Nordmann (1832) for the eggs of *D. rosaceum* (= *Azygia lucii*). It represents a conspicuous organ of the embryo. Nordman noted the bifid character of the organ, describing it as "eine gleichsam zusammengekrummte, dunkler begrenzte Figur, welche an einem Ende wie mehr oder weniger gespalten ershien." All subsequent descriptions of the larva of *A. lucii* consider the organ as simple, sac-like in structure and it has been interpreted as representing a simple type of intestine. In one case, in eggs of *O. cestoides* the body appeared to be split into three rounded lobes (Fig. 32). Even while the embryo is still in the egg, a more or less circular lighter area can be made out within the "lobes" of this organ, an appearance suggesting the presence of a lumen in each. The *Hüllmembran* of Schauinsland (1883) can be found in stained material. It is a thin membrane containing a few flattened cells. It is left behind in the egg shell at time of hatching.

The miracidium is non-ciliated and normally pear-shaped, with a narrow anterior region. Its shape is continually changing, however, as the worm-like movement of the larva results in alternate expansion and contraction of the body. When at full length the shape is narrow and elongate, reaching a maximum of 90 to 100 $\mu$ ; when fully contracted the body becomes spherical and about 45 to 50 $\mu$  in diameter. The posterior end is sometimes pointed. The anterior end of the larva is pulled in and pushed out simultaneously with the contraction and extension of the body. The action of this narrowed anterior region is exactly like that of a proboscis. The earliest movement noted within the egg can only be described as an indefinite "squirming." At no time is there any indication of ciliary movement.

The process of hatching was observed several times. At this period, the movement of the larva has become very definite and like that of the free miracidium, consisting of the alternate pulling in and pushing out of the somewhat pointed anterior end. The movement results in a series of pushes or blows directed at the operculum which sooner or later opens and the worm slides out. The ease of hatching seemed to vary considerably. Thus, one case was observed when the entire process of hatching required only about 30 seconds and almost without effort on the part of the embryo. Another case studied showed a very active embryo which did not succeed in hatching even after several hours and finally its movements slowed down and ceased. Focusing showed that this animal did not seem to be accurately

oriented in the shell and the force of the propulsion of the proboscis was directed a little to one side of the operculum. Although there was ample space for the worm to change its position, it seemed to persist in directing its "blows" at one spot. With the escape of the embryo from the shell, a small stream of minute granules is also given out. These particles attracted small infusorians in the culture and sometimes an empty egg shell would be well filled with small ciliated protozoa.

The body of the miracidium is covered by a very thin cuticula-like layer which is non-ciliated. About the anterior end is a region of bristles or spines. Such an occurrence of spines is common in non-ciliated miracidia. In *Azygia lucii* they are described as occurring on four plates (Borstenplatten) surrounding the anterior end of the larva. This *Azygia* larva also has a posterior series of four bristle plates. Although Odnher (1911b) states that "Borstenplatten" are not present in the genus *Otodistomum*, the spiny areas were very conspicuous in living material. They were also discernible in toto-mounts and could occasionally be definitely made out in sections of embryos within the eggs. Unlike their condition in *A. lucii*, these bristles occur on five strips or areas radiating from the anterior tip. Each strip is tapering in form, being broadest posteriorly. The bristles are longer near the tip and gradually become shorter posteriorly. When the larva first hatches these strips or plates of bristles lie quite flat. Very soon, however, they become loosened at the anterior end and peel off backwards. This shedding of the bristle-plates often gives to the miracidium a very peculiar appearance, as the strips remaining attached posteriorly resemble appendages. The strips are of a very thin epiderm-like material, and when free from the larva tend to curl slightly (Figs. 34 and 43). The process of shedding the strips can be compared in a homely way with the peeling of a banana.

Creutzburg (1890) in his work on the life history of *Dist. ovocaudatum* (= *Halipegus ovocaudatus*) which has a larva very much like that of *O. cestoides*, found that the miracidium of that species lost its coat of bristles only after it had pierced the intestinal wall of a snail. While he does not mention any localized areas of the bristles he describes the shedding of the epiderm as proceeding from the head end. He says (p. 22) the embryo "verwandelt er sich, . . . durch Abwerfen der äusseren stacheltragenden Bedeckung, deren Loslösung nach meinen Beobachtungen zunächst am Kopfpol vor sich geht. . . ." It is therefore quite possible that the spiny region normally serves to aid the miracidium in piercing the tissues of the host. In my material, only one live individual was seen which seemed to have completely shed the bristle plates.

Larvae were usually closely associated with the empty egg shell from which they emerged. The posterior end of the larva seemed to show a tendency to adhere to the egg shell. Only a few larvae were seen at any

great distance from their egg shells. Locomotion was certainly very limited and even the most active larvae progressed very little, if any, in the watchglasses wherein they were studied. The anterior end seemed to adhere rather tenaciously to any debris with which it came in contact (Fig. 34).

The only conspicuous organ of the larva is the structure already mentioned as visible in later egg stages. It extends to about the middle of the body and has a paired sac-like appearance. In one favorable specimen it was observed that leading forward from this organ is a minute duct which opens at the extreme anterior tip of the larva. This anterior tip when free from the bristle-plates is rounded and knob-like in shape. The rounded lighter areas in the central part of each of the lobes of the organ have the appearance of lumens, and the impression gained from study of live material is that the entire organ represents a bi-lobed or bifid intestine. Such a conclusion is supported by the fact that many miracidia have been described as possessing a simple type of intestine. Furthermore, what is certainly the same structure in similar larvae (miracidia of *A. lucii*, *H. ovocaudatus*), has been commonly interpreted by Looss, Leuckart, Creutzburg, Schauinsland, and others as an intestine.

Stained material, and especially sections through mature eggs, present evidence which seems to warrant questioning very seriously the conclusion that this organ represents any form of intestine. In the first place, the organ is found to consist not of two parts but of four. The outline of these "lobes" or parts stains with hematoxylin clearly. The bifid appearance is explained by the fact that the four parts are arranged in pairs (Figs. 36 and 38). The elements of a pair are closely associated, but the pairs may be wide apart (Fig. 38).

Furthermore, the central region (of each lobe) which had been interpreted as a lumen, invariably stains darkly like a nucleus. The granular appearance of the organ in life disappears in sections and in its place is seen a clear transparent area. Safranin staining gave results similar to those obtained with various hematoxylin stains. In fact, safranin stains brought out the four-partite and four-nucleate condition even more clearly than hematoxylin.

The fact that the organ is made up of four similar parts, and that the central regions stain like nuclei make it seem more probable that the organ is not an intestine but a group of unicellular glands. One bit of evidence in favor of viewing the organ as an intestine has been the reported occurrence of a minute pharynx or muscular region about the duct. Only the slightest suggestion of such a structure was detected in the present studies although no special staining of live material was attempted. Von Linstow (1890) reports what appears to be a similar structure in *D. cylindraceum* as a "Stutsapparat." Schauinsland (1883), however, describes and pictures

a minute pharynx-like structure in the larvae of *Azygia lucii* and other trematodes. He does not hesitate to consider such a structure as a true pharynx and the sac-like organ as an intestine. It is interesting to note that in no case does he show any form of cellular structure around the so-called intestine, nor does he show that any lumen is present. On the contrary, he does represent nuclei-like bodies within the intestine in *A. lucii* larvae. It is quite evident that these are the same type of bodies which stain like nuclei in my sections. Schauinsland refers to them as "Kerne im Darminhalt." In one case, he reports "Im Darm bemerkt man 3 Kerne." Both for the larva of *A. lucii* and for the larvae of the other forms he studied, Schauinsland shows from one to four nuclei within the contents of the intestine.

Looss (1894) shows the same condition in his figures. Particularly interesting is his figure of the larva of *A. lucii*. Here three rounded bodies are clearly present within the organ interpreted as an intestine. In the present studies *Azygia* material was found to be most favorable in sections of *A. acuminata*. Here were found four apparent nuclei within the organ in question (Fig. 44). The organ seemed to be simple and sac-like in shape. Because of the much smaller size of the larvae in *Azygia* species it would be very difficult if not impossible to make out the four-partite condition which the larger larvae of *Otodistomum* reveal.

The miracidium of *Schistosoma japonicum* possesses in addition to a sac-like intestine with four nuclei, a pair of large "cephalic glands," one gland being located on each side of the intestine. The glands are nearly as large as the intestine. The four-partite condition found in *O. cestoides* showed, however, no such differentiation between the parts.

Creutzburg (1890) has given not only a description of the appearance of this organ in the similar larva of *Halipegus ovocaudatus* (= *D. ovocaudatum*), but also a history of its fate in later development. In the larva he studied, the organ seemed to be simple and sac-like in form. He says (p. 21): "Dieser körnige Inhalt zeigt oft bläschenähnliche Einschlüsse, die auf das Vorhandensein eines Lumens schliessen lassen." This larva (which does not hatch until the egg has been eaten by a snail) penetrates the intestinal wall of the snail. Soon after it has passed into the body cavity of the snail the larval "intestine" or organ in question begins to diminish in size and finally disappears. Creutzburg says (p. 21): "Die weitere Entwicklung des schlauchförmigen Organs lässt sich noch bei den Sporocysten verfolgen, wo es, seine ursprüngliche Lage am vordern Körperende beibehaltend, späterhin an Grösse allmählich abnimmt, und schliesslich ganz verschwindet." Creutzburg himself was somewhat uncertain as to the correct interpretation of the organ, but in view of its similarity to so-called intestines in other miracidia he concluded it represented a rudimentary intestine.

The conception of an intestine implies the presence of a cellular wall and a lumen. In none of the above instances has either of these conditions been demonstrated. That the organ in question might be interpreted as a group of uni-cellular glands seems more justified. This latter view would be more in accord with the nuclear-like content noted in present material and also described by Schauinsland and others. It would also explain the four-partite condition shown in Figures 36–38 and 40–41. These divisions of the organ into more than two parts seem to offer the strongest evidence against its interpretation as an intestine. Furthermore, if the possible glandular secretion served to aid penetration into the intermediate host, the gradual disappearance of the organ after this act was accomplished in the case of *H. ovocaudatus* would be explained. The tendency showed by the larvae of *O. cestoides* to cling to debris at their anterior ends will be recalled.

While it is true that the miracidia of many trematodes require no glandular secretion in order to penetrate their host, yet it should also be remembered that most miracidia are strongly ciliated and an effective boring force is attained by the action of the cilia which supply a constant forward pressure. On the other hand, the propulsive force of the miracidia-form under consideration is quite different in that when the force is directed against an object the entire body of the larva tends to be pushed backward. As the contents of the intestine of a snail are probably less resistant than the intestinal wall, the physical power of unciliated miracidia would seem to be less effective in this first tissue penetration than is such power in ciliated miracidia.

Unciliated miracidia of digenetic trematodes are very rare. Except among the Azygiidae they are definitely known only in *Halipegus ovocaudatus*. Von Siebold as early as 1837 described an unciliated miracidium for *Dist. variegatum* (later *Dist. cylindraceum* = *Haplometra cylindracea*) but later workers disagreed with this conclusion. Schauinsland (1883) found the larva to possess a coat of cilia which it shed at time of hatching. Von Linstow (1890) found that the shedding of the ciliated coat was due to premature hatching, and that the larva is normally free-swimming. Willemoes-Suhm (1871) described the miracidium of *Ptychogonimus megastomus* and showed it to be very similar to Otodistomum larvae, possessing bristle plates and no cilia. The non-ciliated larvae of *Azygia lucii* and *Halipegus ovocaudatus* have been best known. Leuceruthrus now remains the only genus of the Azygiidae whose miracidium has not been studied.



## NOTES ON THE LIFE HISTORY OF *OTODISTOMUM* *CESTOIDES*

The very thick shell of the egg in *O. cestoides* indicates that these eggs possess the capacity for waiting a long period of time before hatching. On the other hand, the mature larva within the egg at the time of oviposition shows that under favorable conditions the egg may hatch immediately. The further fact that the miracidium lacks the power of locomotion indicates that the eggs do not normally hatch until eaten by a snail. Schauinsland (1883) believes that such is normally the case for *Azygia lucii*, the eggs of which he found hatching in the intestine of a snail. Leuckart (1886:66-67) says that this condition is probably true for all unciliated miracidia. He states: "unter den Arten mit glatter Embryonalhaut scheint es doch manche zu geben, die im Wasser entweder gar nicht oder doch nur selten ausschlüpfen, vielmehr solches vermuthlich erst dann thun, wenn sie, noch umschlossen von der Eischale, in den Darm eines geeigneten Trägers gerathen sind. So sah ich die Embryonen des *Distomum ovocaudatum* niemals im Freien ausschlüpfen, obwohl ich die schon im Mutterleibe vollständig sich entwickelnden Eier wochenlang, bis zum Absterben, im Wasser cultivirte. Eine ähnliche Beobachtung machte Schauinsland an *Dist. tereticolle*, dessen Embryonen im Darne von *Lymnaeus palustris* und *L. stagnalis* noch nach 24-36 Stunden lebhaft umherkriechen, aber im Wasser nur selten frei werden."

The larvae of *Halipegus ovocaudatus* after hatching in the intestine of the intermediate snail host develop into sporocysts as shown by Leuckart and Creutzburg. The explanation of the ready hatching of the eggs of *O. cestoides* in sea water is found in the effect of the changes in concentration of the sea water due to evaporation. This effect was accidentally discovered when a culture of mixed eggs was left exposed in a watch glass for several hours. Evaporation of the sea water caused the opercula of the eggs to open whereupon the larvae, even though immature, partially escaped. The same result was repeatedly noted when sea water containing eggs was allowed to evaporate. The more mature eggs hatch more readily and the larvae appear active and healthy. When the evaporation is pronounced the less mature eggs open and the embryos partially slide out from the shell. Embryos thus prematurely hatched show no movement. Young eggs wherein the body form of the embryo is not definitely established do not open. In regular cultures the evaporation was slight and gradual, so that only mature eggs were stimulated to hatch.

Still further evidence that the eggs do not normally hatch in a free state is furnished by the following data: Three vials of fresh eggs were covered with an animal parchment membrane and immersed in a large aquarium of running sea water. Here any change of concentration due to evaporation would be negligible. Although all of these cultures were examined at intervals for about a week, no hatched eggs or larvae were found, while eggs collected at the same time but kept in open vials hatched with customary regularity. This experiment to eliminate evaporation was tried with the purpose and hope of increasing the hatching of the eggs. The fact, however, that this more normal environment of the eggs reduced or eliminated hatching is in full accordance with the later discovered cause of hatchings by evaporation of the sea water.

The opening of the operculum of the egg shell therefore seems to be induced directly or indirectly by an increase in density or osmotic pressure in the surrounding medium. The indication is that the stimulus is primarily a physical one rather than a chemical one. That is, increased density in the content of the snail's intestine as compared with the density of sea water, rather than any chemical peculiarity of the location within the snail, induces the hatching of the eggs. This conclusion receives support from Schauinsland's experiments in hatching the eggs of *A. lucii*. He obtained normally laid eggs, and found that the speed of their hatching could be greatly increased by placing them in a solution of common salt. In this solution the eggs hatched in about 15 minutes or practically immediately. It seems clear that no particular chemical substance is necessary for the stimulation to hatch, but merely an increase in osmotic pressure in the surrounding medium. Whether such a stimulus to hatch is direct or indirect is, of course, unknown. It is possible that the discrepancy in densities within and without the egg shell stimulates a secretion from the gland cells of the embryo, and that this secretion is the direct cause of the opening of the operculum. Some evidence in favor of this possibility is seen in the fact that even excessive evaporation does not cause the younger eggs to open although the operculum is well defined in the one-celled egg stage.

Various molluscs common in the vicinity of Frenchman's Bay were kept in vials of egg cultures. After periods varying from about 12 hours up to several days, these molluscs were removed and examined microscopically by means of smears. In general, all of this work was unsatisfactory. Eggs retained between the shell and body of a snail showed a tendency to hatch after the snail had been out of water for some time. This result would be expected, being probably due to sea water evaporation. There was no evidence that larvae so hatched penetrated the tissues of the snail. Unfortunately, during most of the work, no special examination was made for the presence of eggs in the intestine. One very conspicuous case was

discovered, however, when it was found that *Littorina litorea* ate these eggs very readily. Pellets of fecal or food matter in the intestine showed eggs present in large numbers. The snail had been kept for four days in a vial containing eggs. One pellet from the intestine contained over 50 eggs, another 25, 15, 12, etc., down to 4 or 5. A live larva was found by lightly crushing one of these pellets under a cover glass. The location and condition of this larva leaves no doubt that it had recently hatched from one of the eggs in the intestine of the snail. The snail had been dry and out of water for about a day and a half. Two out of six other specimens of *Littorina* examined by smears showed eggs in the intestine. This condition was further investigated by examination of serial sections of snails exposed to eggs. All of four specimens of *Littorina* so sectioned showed numerous eggs in the intestine. These eggs sometimes occurred in large numbers (several hundred). One case of a partly hatched larva was discovered in these sections. Careful examination revealed no certain case wherein such larvae had penetrated the wall of the intestine. Serial sections of two specimens of *Thais lapillus*, one of which had been in a very vigorous culture for over a week, gave practically negative results. Occasionally, isolated eggs were found in the digestive tract of one of these specimens, while the other contained no eggs. Sections of *Buccinum undatum* (which had, however, been in the egg culture only one night) showed no eggs.

An encysted distome was not uncommon in both *Littorina* and *Thais*, but it could not be determined as *Otodistomum*. It occurred in thin walled cysts near the digestive tract. Redia and cercaria were also found in these snails, but probably those discovered did not belong to *Otodistomum*. No definite conclusions can therefore be drawn in regard to the first intermediate host, except that some species of snails (especially *Littorina*) readily devour the trematode eggs, and that these eggs can hatch in the intestine of the snail. Other species of snails under similar conditions seem to eat very few or none of the eggs.

In the meantime, rather conclusive evidence has been found in regard to the last intermediate host of this trematode, at least in European waters. Scott (1909), in his report on fish parasites of Scotland waters, states in his discussion of *Dist. cestoides*: "Several young specimens of a *Distomum*, which closely resembles the immature *D. cestoides* from the skate, were found encysted on the walls of the stomach of a Witch Sole, *Pleuronectes microcephalus*, captured in Moray Firth. There were several cysts observed, and all those examined contained only young *Distomids*—in some cases one, in others two examples.

"Fishes form a considerable proportion of the food of large skates, and probably the Witch Sole, which lives in moderately deep water, sometimes becomes the prey of these large Plagiostomes."

Nicoll (1913a) records *Otodistomum cestoides* (van Ben.) from *Raia macrorhynca* and adds the following: "In regard to the life history of this species, it is probable that the cercaria discovered by Scott, encysted in the stomach wall of the witch, *Pleuronectes cynoglossus* (in Scott's paper this species is inadvertently named *P. microcephalus*) represents the larva of *O. cestoides*. In the same fish I have found encysted in the wall of the stomach a cercaria, which from its large size and general structure, cannot be referred to any other species. It occurred as a large orange-yellow globular cyst 1.95 mm. in diameter, firmly attached to the outer wall of the stomach by a short pedicle. The wall of the cyst consisted of a thick, tough outer coat within which was a large amount of viscous yellow material. The cercaria measured 2.4 mm. in length, with a maximum breadth across the ventral sucker of 0.66 mm. Both suckers were transversely elongated, the oral measuring 0.29 by 0.35 mm. and the ventral 0.43 by 0.59 mm. The latter was situated at a distance of 0.96 mm. from the anterior end. The pharynx was small and situated close to the oral sucker. There was a very short esophagus and wide diverticula extending in a slightly sinuous manner to the posterior end of the body. The excretory vesicle was Y-shaped and consisted of a median stem extending a quarter of the length of the body, and two lateral branches reaching forward as far as the pharynx. No other organs were visible."

This cercaria described by Nicoll resembles almost exactly my youngest forms from the skate. A copy of Nicoll's figure is given for comparison (Figures 2 and 3). As Nicoll points out, no other trematode is known to which this cercaria could belong except *O. cestoides*. Reference to my records shows that the sand dab and flounder are among the most common fish food of the big skate. No cysts were found containing cercaria, but relatively few of these flat fish were examined. It is very probable that the sand dab or flounder conveys the trematode to the big skate. The degree of infection and range of size of the parasite in the skate indicating a continuous infection is in accordance with this conclusion.

The immature trematode found encysted in the stomach wall of *Lophius piscatorius* and named "*Xenodistomum melanocystis*" by Stafford appears to be an immature *O. cestoides*. It is so identified by Odhner (1911b), who concludes that the goose-fish does not represent a true intermediate host, but that the cysts in that host represent an accidental infection.

## SYSTEMATIC REVIEW OF THE FAMILY AZYGIIDAE

The characteristics of the family Azygiidae as given by Odhner (1911b: 513-14) are as follows:

Mehr oder weniger langgestreckte und abgeplattete "Distomen" mit einem derben, muskelkräftigen Körper von 5-75 mm. Länge. Saugnäpfe sehr kräftig entwickelt, einander genähert. Haut unbewaffnet, mit dicker Cuticula, die sich beider Kontraktion in unregelmässige Querfalten legt. Darm mit kräftigem Pharynx, äusserst kurzem Oesophagus und bis ins Hinterende reichenden Darmschenkeln; ein Präpharynx fehlt. Excretionsblase Y-förmig mit sehr langen, bis ins Kopfende reichenden (und sich dort mitunter vor dem Mundsaugnapf vereinigenden) Schenkeln. (Bei *Ptychogonimus* ist der Hauptstamm sehr verkürzt.) Genitalporus median, zwischen den Saugnäpfen. Die charakteristische Entwicklung der Endteile der Geschlechtsweg bietet die beste Bürgschaft für die nahe Verwandtschaft der in diese Familie zusammengestellten Gattungen: der Genitalsinus ist sehr geräumig entwickelt; die männlichen Leitungsweg bestehen aus Ductus ejaculatorius, Pars prostatica und Samenblase, die beiden letzteren schlauchförmig und ausser bei *Ptychogonimus* von einem Cirrusbeutel umhüllt; die ganze Komplex liegt unmittelbar vor oder über dem Bauchsaugnapf. Ovar und Hoden median, unmittelbar hintereinander in Hinterkörper gelegen. (Ausnahme: *Leuceruthrus*.) Uterus von Ovar aus nach vorn ziehend (Da er bei *Ptychogonimus* vor dem Ovar zuwenig Platz für seine Entfaltung findet, sendet er jederseits zwischen den Geschlechtsdrüsen und Dotterstöcken eine lange Schlinge nach hinten bis in die Nähe des Hinterendes). Laurerscher Kanal vorhanden, Receptaculum seminis fehlt. Dotterstöcke follikulär entwickelt, in den Seiten des Hinterkörpers, nicht bis ins äusserste Hinterende reichend. Vagina vorhanden. Eier etwa 0.045-0.085 mm. lang, gedeckelt; sie enthalten bei der Ablage ein reifes, anscheinend immer unbewimpertes Miracidium.—Magenparasiten bei Fischen.

Odhner included the following genera in this family: *Otodistomum*, *Azygia*, *Leuceruthrus*, and *Ptychogonimus*. *Azygia* and *Otodistomum* are the most nearly related genera. *Leuceruthrus* has a very different arrangement of gonads, and Goldberger (1911:7) suggested that it might represent the type of a new family. In this genus the testes are lateral and anterior, being far removed from the median and more posterior ovary. Odhner, however, shows that this forward migration of the testes is of secondary importance, compared with the similarity which the genus shows to *Azygia* in the character of the genital atrium. *Ptychogonimus* shows the most marked deviations from the family type. These deviations lead toward certain characteristics of another group of marine trematodes known as the *Distomum-clavatum* group. Consideration of this relationship might be of value in determining the systematic position of the family Azygiidae.

Trematodes of the *Dist. clavatum* group are also of large size with powerful, muscular bodies, and are found in the stomachs of marine fish. The group, containing a number of species, has been an isolated one

taxonomically. In 1911, Odhner placed the group as a sub-family of the Hemiuridae. Although designating these forms as of sub-family rank, he did not give a sub-family name. Nicoll (1915) in his list of trematodes of British fish, classified them under the Accacoeliinae. The term "Dist. clavatum group," although awkward, is curiously persistent. The species in question (*Dist. clavata* (Menz.) Rud.) is actually *Hirudinella clavata* as designated by Blainville in 1824. Blainville later included also in this genus the former *Fasciola ventricosa*. The forms have been usually referred to the genus *Distomum*. All species in the group probably belong to the genus *Hirudinella*.

Similarities of this group to the Azygiidae in general are: large size, muscular bodies, no pre-pharynx, very short esophagus, similar excretory system, and similar genital atrium. This latter condition forms a very important and striking resemblance. Jägerskiöld (1900) describes the genital sucker of *Distomum megastomum* (= *Ptychogonimus megastomus*) as "ein neuer Typus von Kopulationsorganen." He compares the terminal genital regions of *D. veliporum*, *D. clavatum*, *D. verrucosum*, and *D. megastomum*, and offers the suggestion that the latter (which now represents the genus *Ptychogonimus*) is phylogenetically derived from a form resembling *D. veliporum* through a series now represented by members of the *Dist. clavatum* group. This suggestion is based solely on comparison of the "Kopulationsorganen." The comparison does show that so far as the distal genital apparatus is concerned, *Ptychogonimus* is more similar to the *Hirudinella* group than to the genera of the Azygiidae. This similarity is marked not only by the more conspicuous folds and muscle rings in the wall of the atrium, but also by the fact that both sex ducts open separately on the genital papilla in *Ptychogonimus* and in *Hirudinella*.

The lack of a cirrus sac in *Ptychogonimus* is another important feature in which that genus is like *Hirudinella* and different from other Azygiidae. Furthermore, the uterus in *Ptychogonimus* sends two coils posterior to the ovary and extending nearly to the posterior end of the body. This distribution of the uterus is unlike anything found in other Azygiidae but very similar to the condition in *Hirudinella*.

Odhner's distinction between the Azygiidae and the *Hirudinella* group is that in the latter not only have the testes migrated forward (as in *Leucerthus*) but the ovary has followed also. The ovary is then located directly behind the testes instead of in front of them as is the normal condition in the Azygiidae. He continues (p. 524): "—dadurch werden also die Lagebeziehungen zwischen Ovar und der Hauptmasse des Uterus die umgekehrten zu denen der Azygiiden. Nach diesem zweifellos recht schwerwiegenden Merkmal habe ich in erster Linie die Familiengrenze gezogen."

However, as two coils of the uterus extend posteriad in *Ptychogonimus*, in this genus also the chief mass of the uterus is posterior to the ovary as can readily be seen from the figures of Jacoby (1899). One of the chief distinctions, then, between this genus and the *Hirudinella* group seems to be the position of the ovary in relation to the testes. Yet the significance of gonad location was discounted by Odhner himself when he included *Leuceruthrus* in the Azygiidae. *Ptychogonimus*, however, possesses follicular vitellaria as in *Azygia*, and not tubular as in *Hirudinella*. Again, its body is flattened and less muscular than *Hirudinella*. Considering these latter features, the genus is probably more appropriately considered as a member of the Azygiidae. Yet evidently it shows a relationship between the two groups and through it the family Azygiidae leads to the Hemiuridae and to a sub-family near the Accacoeiliinae.

The miracidium of *Ptychogonimus* is non-ciliated and bears a spiny anterior region as does the miracidium of *Azygia*. Odhner considers *Ptychogonimus* to be more closely related to *Azygia* than to *Otodistomum* "namentlich auf Grund des Baues der Miracidien." It has, however, already been shown that *Otodistomum* larvae are also equipped with bristle-plates. This inference of relationship between genera on the basis of larval forms is interesting. No description of the miracidia of *Hirudinella* species could be found, but, judging from sectioned material of *Hirudinella fusca*, the mature eggs in this species do not contain larvae at all similar to those contained in mature eggs of *Otodistomum*. Hence, the first larval form of *Ptychogonimus* probably relates that genus more closely to the Azygiidae than to *Hirudinella*, if similarity of larval forms is reliable evidence. But there is reason to believe that similarity in miracidia of different species does not necessarily indicate close specific or even generic relationship of the adult trematodes. Thus, the miracidium of *Halipegus ovocaudatus*, a parasite of the frog, has the very same morphological features that characterize the miracidia of *Azygia* and *Otodistomum*. It is of the same shape and movement, is unciliated, possesses bristle plates, and has the so-called "intestine" (Creutzberg, 1890). Yet the adult form of *Halipegus* is not closely related to *Azygia*. The natural explanation is that the adults have undergone evolution independently of their larval forms. The non-ciliated miracidium is probably always associated with the fact that the egg normally hatches only after eaten by a snail. The retention of this feature in developmental history results in the retention of a certain type of larva. In the meantime, the adults (in the two cases cited) seem to have evolved along different lines without change in their miracidia. That is, one finds here the very common condition of constancy of larval forms and divergence of adults. The other possibility of convergence of larval forms is not probable in this case because the miracidia resemble each other in such great detail.

The genera of the Azygiidae can be separated by the following key:

Uterus sending coils posterior to ovary.....	Ptychogonimus
Uterus entirely anterior to ovary	
Ovary and testes more or less directly behind one another in median line	
Genital pore close to acetabulum, branches of excretory system separate.....	Azygia
Genital pore nearer oral sucker, branches of excretory vesicle united anterior to oral sucker.....	Otodistomum
Testes lateral and anterior to ovary.....	Leuceruthrus

Ptychogonimus has the single species *megastomus*. *Leuceruthrus micropteri* is the only representative of the genus *Leuceruthrus*.

The two species of *Otodistomum* have already been considered at length. The egg size is the most certain distinction between them.

Eggs averaging about 69 by 46 $\mu$ .....	<i>O. cestoides</i>
Eggs averaging about 86 by 58 $\mu$ .....	<i>O. veliporum</i>

A key to the species of *Azygia* will follow later.

*Azygia* is the only genus of the family showing taxonomic confusion in its species. As it is morphologically very similar to *Otodistomum*, some of the difficulties leading to confusion were encountered in the present studies, and led to further comparative study of different species of *Azygia* as well as of the two genera themselves. These difficulties involved the question of relative significance of such factors as: body size and shape; extent and arrangement of the vitellaria; relative size and position of the suckers; shape of pharynx; position of gonads; and size of eggs.

In the first place it is important to note that these forms are all very muscular and highly contractile. Their nature in this respect can be contrasted with such forms as *Dicrocoelium* and *Opisthorchis*, so that even though the internal arrangement of organs may be similar, the heavy muscular body sharply distinguishes the *Azygia* group from them. Looss noted this fact in 1899 when he pointed out that the common descriptions of *A. lucii* (= *Dist. tereticolle*) hardly separated it from the genus *Opisthorchis*. Yet *Opisthorchis* is a delicate, quite muscularless form, and not closely related to *Azygia*.

Body contraction in the *Azygia* group where the worms are elongate in form not only alters the general shape, but it also changes the relation of the ovary and testes so that the former may lie almost lateral to the anterior testis, instead of directly anterior to it. In spite of the fact that Goldberger (1911) noted this variation in his *A. acuminata*, he nevertheless separated his genus "*Hassalius*" upon this condition. The genus *Hassalius* has already been rightly reduced to synonymy with *Azygia* by Odhner (1911b) and by Ward (1917). Moreover, body contraction results in throwing the intestinal ceca into folds, giving them a zig-zag appearance.



Such an appearance is entirely without significance except as it indicates to some extent the degree of contraction. It should be eliminated as a distinction between species. A pointed or blunt caudal region is also a character depending largely upon temporary body contraction.

Some confusion among genera and species is also due to a rather extreme range in size exhibited by the trematodes of this group. The conspicuous growth of *Otodistomum cestoides* even after arrival at sexual maturity, has already been considered. While this feature is common among trematodes, it seems to be particularly prominent in *Azygia* species. Odhner is therefore justified in considering Stafford's genera, *Megadistomum* and *Mimodistomum* (which were largely based on body size) as synonymous with *Azygia*.

The extent and arrangement of the vitellaria are often very constant in trematodes. In the *Azygiidae*, the vitellaria are less reliable for specific diagnosis than might be expected. The variability of these organs in *O. cestoides* has been noted in detail. Odhner allows them almost unlimited range in *Azygia* species also. Certainly the importance given to details of these organs by Goldberger has been unwarranted. In the present studies, the constancy of the vitellaria in the various forms was critically studied, and will be considered in connection with the different species.

One histological feature of special interest in highly muscular trematodes such as the *Azygiidae*, is the arrangement of body muscles. Body muscles in trematodes usually consist of certain layers (circular, longitudinal, and diagonal) immediately beneath the cuticula. In addition to these muscle layers of the body wall, there occurs in the present group a well developed layer of longitudinal muscles within the parenchyma. These muscles running parallel with the longitudinal muscles of the body wall occur in bundles forming a more or less compact layer, so that in cross-section there is separated a central region containing most of the organs from an outer cortical region. Ward (1910) called particular attention to these muscles in *Azygia sebago*. They were also described and figured by Leuckart (1886) for *Azygia tereticolle*. Concerning them Leuckart (p. 18-19) says: "Unterhalb des Hautmuskelschlauches ordnen sich diese Parenchymfasern hier und da wieder in förmliche Schichten, wie z.B. bei *Distomum tereticolle*, bei dem sich in einiger Entfernung von den Diagonalmuskeln der Rinde eine scharf begrenzte zweite Längsfaserschicht bildet, die aus kräftigen Spindelzellen besteht und mit Ausschluss der Dotterstöcke die in dem hellen, von Bindegewebe erfüllten Zwischenraum zwischen ihr und dem Hautmuskelschlauche zu liegen kommen, sämtliche Eingeweide in sich einschliesst." Thus, the vitellaria occurred outside the muscles, as Ward found for *A. sebago*. In the present study of different American forms of *Azygia*, the vitellaria always occurred outside this muscle layer. The

available sections of Goldberger's *A. acuminata* showed the muscles less developed and more widely scattered.

The occurrence of similar body muscles in *Otodistomum* serves as an additional histological link of relationship between these forms and *Azygia*. Villot (1879:7) describes the grouping of such muscles for *D. insigne* (= *Otodistomum veliporum*). He says: "Une dernière couche de fibres longitudinales disséminées dans la zone limite du parenchyme. Ces fibres sont très-fortes." Villot's figures clearly show these muscles as a definite layer. They represent a condition similar to that found in *Azygia* species, but their position is distinctly different in *Otodistomum* where they completely enclose the vitellaria. My own studies on *Otodistomum cestoides* and *O. veliporum* show the muscles present in a discernible layer but more scattered than in *Azygia* species, and external to the vitellaria.

What may represent a homologous arrangement of longitudinal muscles has also been described for trematodes of the *Hirudinella clavata* (= *Distomum clavatum*) group. These forms are extremely muscular and contractile. In the neck region of *H. clavata* the following muscle layers occur: circular layer, longitudinal layer, oblique layer, and finally another internal zone of longitudinal muscles. Concerning this latter, Poirier (1885:483) says: "Celle-ci se compose d'un grand nombre de faisceaux musculaires souvent très gros, et formés de fibres longitudinales d'un fort diamètre." Poirier describes a rather peculiar condition posterior to the ventral sucker. In this region, he says (p. 484): "toutes les zones de fibres musculaires à l'exception de celle des faisceaux longitudinaux internes, ont complètement disparu. Cette dernière, par contre, a pris un développement considérable. Elle est formée de faisceaux composés d'un grand nombre de fibres, très serrés les uns contre les autres, de façon à former une gaine épaisse, à peu près continue, à l'antérieur de laquelle se trouvent le parenchyme du corps et les différents organes de l'animal."

I have found (in agreement with Mühlischlag, 1914) a similar condition in *Hirudinella fusca*. The other body muscles, however, do not here completely disappear as recorded by Poirier. Throughout the body length in this form there occur from the cuticula inward the following muscle layers: (1) circular, (2) longitudinal, (3) circular, (4) longitudinal. Layer (2) is always very weak with only scattered fibers. In mid-body region, layer (4) is very powerful with heavy fibers grouped in large bundles. It is this inner layer which is possibly homologous with the internal parenchyma muscles of *Azygia* and *Otodistomum*. It differs from them in being immediately surrounded externally by a ring of circular muscles. Granting that these muscles are present in all three groups, they differ in *Azygia* species by being located *internal* to the vitellaria, whereas in *Otodistomum* and *Hirudinella* they are found *external* to the vitellaria.

The writer has been fortunate in obtaining for study type or original material of all the different *Azygia* forms described from America with the exception of those recorded by Stafford. Co-type material of *Azygia perryii* Fujita from Japan was also studied. The conclusions reached will be included under the following discussions of accepted species.

*AZYGIA ANGUSTICAUDA*<sup>1</sup> (STAFFORD 1904)

[Fig. 27]

Synonyms: *Mimodistomum angusticaudum* Stafford 1904

*Azygia loossii* Marshall and Gilbert 1905

*Azygia loossi* Odhner 1911

The descriptions of the two above mentioned forms appeared at about the same time. Since in the present work material was obtained only of *A. loossii*, the distinctive specific characters will be taken from that material. Goldberger (1911) has redescribed this species at some length. Reference to Stafford's description will be made a little later.

The position of the gonads in the extreme posterior region of the body seems to be a point in which *A. loossii* is distinct from all other species. In this form the testes are located about 1/7 to 1/8 the body length from the posterior tip. Furthermore, the ventral sucker in this species is only slightly anterior to the middle of the body, whereas in other species it is distinctly more anterior. Such marked differences could possibly be explained by a highly extended anterior region and a highly contracted posterior region. But in the few specimens available, it was very clear that the entire body was extended. The uterus in *A. loossii* appears to be tubular with eggs in linear order, but this condition may be due to the possibility that the specimen had but recently arrived at sexual maturity. The musculature of the genital atrium seems to be particularly well developed in this species, so that the genital pore appears to be surrounded by a small sucker. The eggs average about 52 by 28 $\mu$  which is intermediate between the recorded sizes of eggs in *A. sebago* and *A. acuminata*.

What seems to be an additional important feature of this species is the extent of the vitellaria almost to the region of the ventral sucker. Although the vitellaria actually begin in the mid-body region instead of anterior to it as is common in other species, the fact that the ventral sucker itself is equatorial in position explains the relative proximity of the vitellaria to it. The proportion of body length to distance from ventral sucker to most anterior vitellaria was found to be 27.2 and 26.2, a ratio reached only by *A. acuminata*. (See Table 18.) *A. loossii* was collected

<sup>1</sup> Due to an obvious misprint the name of this species was spelled "augusticaudum" in Stafford's original paper.

from *Micropterus salmoides*, *Lucius lucius*, and *Amia calva* from Wisconsin lakes.

The above characters do not seem to warrant a new genus for this species, as in every important respect it agrees with the genus *Azygia*. It seems quite certain, however, that it does represent the same form described by Stafford as "*Mimodistomum angusticaudum*" from the mouth, pharynx, esophagus, and stomach of *Lota maculosa* and *Stizostedion vitreum*. Stafford describes the ventral sucker "as situated in the middle of the length of the worm in the most normal cases. The genital glands are flattened against each other and crowded backwards near to the ends of the caeca." Comparing it with *Azygia*, he says: "In the 12 mm. *Azygia* I selected as example, the ventral sucker is 2 mm. from the anterior end. In the 7 mm. *Mimodistomum* it is 3.5 mm. from the end, while the relatively long distance between sucker and ovary is in marked contrast to the short distance between the latter and the posterior end of the worm."

Thus, although Stafford's description is brief, the differences he points out are exactly those between *A. loossii* and other American species. That is, there is no point in Stafford's description of "*Mimodistomum angusticaudum*" that does not agree with *A. loossii* and practically every point mentioned is characteristic for that species. If, therefore, Stafford's description is to be accepted there seems to be no escape from considering the two species synonymous.

#### *AZYGIA ACUMINATA* GOLDBERGER 1911

[Figs. 21, 22]

Goldberger unfortunately emphasizes unimportant points (e.g., vitellaria unbroken, ceca zigzag, tail pointed, constricted neck region) in distinguishing this species. A study of his material, together with specimens of the same species collected and identified by Cooper, has led to the belief that this form represents a true species capable of distinction by definite features. A few specimens\* from Dr. Ward's collection from the same host (*Amia calva*) apparently also belong to this species.

Certain similarities in all of the material could be demonstrated. The constriction of the neck just anterior to the ventral sucker appears to be fairly constant and noticeable. This character should not be emphasized, however, as Goldberger's own figure of his *Azygia bulbosa* shows that some slight localized and temporary constriction may occur in this region in other species. The most distinguishing specific characters were found to be: relatively wide body, anterior extent of the vitellaria, egg size, and poorly developed condition of the internal parenchyma muscles. It should be realized that the nature of all of these features is of somewhat precarious

\* Collection of Dr. H. B. Ward, vials Nos. 25.27 and 25.28.

standing in this genus. Probably no one of them, unless very marked, would justify a recognition of a separate species. Only because of the general association of all of these characters can the forms be separated from the other common American species. It may also be of some significance that all of the material is from the same host, *Amiatus calvus*.

The proportion of body width to body length can be seen in Table 15. This point cannot be considered a reliable specific character. Generally speaking, *A. acuminata* usually shows a wider body than most of the other forms.

In nearly every case, the vitellaria began at about the level of the posterior edge of the ventral sucker, rarely appreciably posterior to it. In none of the other American species was this general condition found except in *A. angusticauda* (Staff.) wherein this matter has already been discussed. Table 18 compares *A. acuminata* with the other forms in this respect.

The average egg size of twenty measurements from Cooper's specimens was 64.8 by 28 $\mu$ . The average egg size of about fifty measurements from Goldberger's specimens was 63.4 by 34 $\mu$ . The egg size in Ward's material was 63 by 29 $\mu$ . All of these averages are considerably above the egg size of the most nearly related *Azygia* species (Table 14). This large size is attained in the largest specimens of a few forms (like Leidy's *Dist. longum*), but was never found in specimens of sizes similar to *A. acuminata*.

Four sectioned specimens (three from Goldberger's material, and one from Cooper's) agreed in showing a much more scattered and less compact

TABLE 9. *Azygia acuminata*  
Measurements in millimeters

Length	Width	Oral sucker	Ventral sucker	Post. edge v. sucker to mid. ovary	Post. edge v. sucker to ant. end	Post. edge v. sucker to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
8.*	1.68	1.	0.75	2.6	3.3	0.4	1.37	0.31	0.31
11.3*	2.5	1.3	1.		3.9	0.65	2.56	1.56	0.96
10.9*	2.5	1.3	0.93	3.4	3.87	0.37	2.5	0.63	1.01
9.75*	1.3	1.	0.68	3.3	3.1	0.5	2.4	0.5	1.5
* 2.5	1.25	1.			3.87	0.74			
9.68*	2.5	1.3	1.	3.	3.75	0.3			
9.87*	2.6	1.25	1.06	3.56	3.62	0.35	1.4	0.65	1.15
6.87	1.8	1.18	0.9	1.9	2.5	0.	1.6	0.78	0.84
6.56	1.75	1.06	0.74	2.3	1.75	0.5	1.6	0.95	0.76
6.3	1.5	0.93	0.78	2.	2.18	0.	1.4	0.84	0.13
7.5	2.	1.18	1.	2.68	2.75	0.	1.68	0.88	1.03
8.87†	1.4	0.87	0.812	2.93	3.3	0.3	2.18	1.5	1.56
9.37†	1.3	0.87	0.812	3.75	3.3	0.75	2.18	0.87	1.18
11. †		0.93	0.75	3.87	4.12	0.5	2.8	1.87	1.9

arrangement of internal, longitudinal parenchyma muscles than was found in the other *Azygia* species.

Table 9 (page 60) gives measurements of the available *A. acuminata* specimens. Those marked \* were collected by Cooper; those marked † are from the Ward collection and were obtained at Fairport, Iowa, in 1916 by T. B. Magath. In each case the host was *Amiatus calvus*.

Pearse (1924) records *A. acuminata* from the "wall-eyed pike" in Lake Pepin, Wisconsin, but gives no further data.

### *AZYGIA LONGA* (LEIDY 1851)

[Figs. 19, 20 and 30]

Synonyms: *Distomum longum* Leidy 1851  
*Distomum tereticolle* of Leidy 1851  
*Megadistomum longum* (Leidy) Stafford 1904  
*Azygia tereticolle* of Stafford 1904  
*Azygia sebago* Ward 1910  
*Azygia bulbosa* Goldberger 1911  
*Hassallius hassalli* Goldberger 1911  
*Azygia lucii* of Cooper 1915

Authentic material of all these forms (with the exception of Stafford's) was obtained. A careful comparative study of this material has led to the acceptance of the above list of synonyms. The occurrence of intermediate conditions between somewhat extreme types, and the high degree of variability of some factors, necessitates the extension of the limits of the species as will be shown. In view of the high degree of contractility and marked growth changes of trematodes in this group, all comparisons were made relative to body length and on the basis of body proportions. Even on this basis consideration must be given to relative changes in proportions with growth.

*Azygia sebago* Ward (1910) from the Sebago salmon is the best described of American species. Leidy's *Dist. longum* reported in 1851 and the various other species recorded from America since 1910 have appeared to differ more or less markedly from *A. sebago*. These differences will now be critically examined.

In separating *A. sebago* from the European species, *A. lucii* (= *A. tereticolle*) Ward emphasized the posterior extent of the vitellaria. Although Odhner (1911b) is partially justified in discounting dependence upon vitellaria in this genus, the distinction seems to be a valid one. Not only in *A. sebago*, but in all American forms of *Azygia* examined, the vitellaria always extend appreciably beyond the hind testis, usually at least half way from this point to the posterior end, and may even reach to the extreme posterior tip as was observed in one case. According to descriptions and figures of *A. lucii*, the vitellaria end in the region of the hind testis and

rarely extend appreciably posterior to it, although van Beneden (1858) says the vitellaria reach "depuis la ventouse posterior jusqu'en dessous du second testicule." His figures show the vitellaria extending beyond the hind testis to a point about  $1/4$  the distance between that organ and the posterior end. Looss (1894:16) describes their extent for the European species as follows: "Die Dotterstöcke erstrecken sich in den Seitentheilen des Leibes ausserhalb der Darmschenkel nach vorn hin nicht bis an den Bauchsaugnapf—sie endigen ungefähr die Länge seines Durchmessers vorher-, nach hinten zu kaum jemals bis über hintere Grenze des zweiten Hodens hinaus."

Further distinction between American species and *A. lucii* can probably be found in pharynx shape, a point upon which Odhner separates a new species, *A. robusta*. The pharynx of American species is more globose than the elongate pharynx of *A. lucii*. This point will be considered in more detail under *A. robusta*.

*A. sebago* averages about 6 to 8 mm. in length. Specimens were found as small as 1 mm. and no ova were present in forms 2.85 mm. long. In regard to sucker proportions: "The ventral sucker or acetabulum is usually distinctly smaller than the oral. In the extreme case it appears about equal in size or, on the other hand, only about half as large" (Ward, 1910:1177). The questions of body size, size at sexual maturity, egg size, and sucker proportion are important points of comparison in American *Azygia* species.

Of the other *Azygia* species, *A. bulbosa* Goldberger is most evidently identical with *A. sebago*. The descriptions of the two forms show no important differences. Type material of both species was studied. Reference to comparative tables (Tables 15 to 18) shows almost identical body size and proportions, as well as similar position and arrangement of organs. Goldberger gives the egg size of *A. bulbosa* as 56 by  $25\mu$ . Although the eggs may reach a length of  $57\mu$ , the average of my 110 measurements gave the egg size as 48.3 by  $28.7\mu$ . Ward gives the egg size of *A. sebago* as 48 by  $27\mu$ .

The original type material of *Hassallius hassalli* Goldberger was also examined for comparison. That all of this material was strongly contracted was made very evident by the ring-like foldings of the cuticula and the excessive foldings of the intestine. Goldberger himself explained the "numerous transverse sulci" of the cuticula as "apparently due to contraction of the worm." The high degree of body contraction is also evidenced by the longitudinal compression of the organs, especially the uterus, gonads, and vitellaria. The pharynx is brought down closer to the ventral sucker than is normal. Yet, in spite of the evident body contraction, Goldberger separates his genus from *Azygia* on a thicker, shorter body form, and a lateral position of the ovary in relation to the anterior testis, both of which characters would be caused by body contraction. The only

comparison Goldberger makes between the two genera is in these words: "This new genus, aside from its external characters, differs from *Azygia* in the position of the ovary, which here is by the side of, that is in the same transverse plane as the cephalic testis, instead of cephalad of the latter as in *Azygia*." The shorter and thicker body shape is directly due to contraction. In regard to the position of the ovary, reference need only be made to Goldberger's figure of *Azygia acuminata* (his Fig. 8) and to the following sentence from his description of this *Azygia* species: "In one of four press preparations, the ovary bears exactly the same relation to the testes as that in *Hassallius hassalli*; that is, it is within the zone of the cephalic testis." In *Azygia* species as in *Otodistomum* (see Figs. 13-18), the ovary may be located slightly to the right or to the left of the anterior testis, and is consequently forced into the "zone" of this testis when the body is contracted. Until the ovary can be shown to be lateral to the testis in uncontracted specimens, this character cannot be given even specific significance.

In fact, after allowance is made for body contraction, this form cannot be distinguished from the other common American forms as represented by *A. sebago* and *A. bulbosa*. Goldberger's own description and figures show the terminal genital apparatus in his *A. bulbosa* and *Hassallius hassalli* to be exactly similar. Study of his publication and original material reveals not a single point of difference between the two forms, except differences that might be due directly to body contraction. Comparison of sagittal sections of this species with sagittal sections of *A. sebago* and the *A. lucii* of Cooper shows no differences that can in any sense be considered specific. Goldberger gives an egg size of 48 by 26 $\mu$  measured from sections. My measurements of eggs from toto mount gave about 49 by 24 $\mu$ , but the larger eggs measured from sections were from 54 to 57 $\mu$  in length by about 24 $\mu$  in width, or practically exactly the measurements for *A. bulbosa*. The internal parenchyma muscles in *Hassallius hassalli* are prominent and are exactly as in *A. sebago* and the *A. lucii* of Cooper.

Leidy in 1851 described *Distomum longum* from the mouth of *Esox estor* (= *E. lucius*). Stafford (1904) designates as "*Megadistomum longum* Leidy" forms which he collected from the mouth, esophagus, and stomach of *Esox masquinongy*. These trematodes are very long, Leidy's specimens being up to 76. mm. (3 inches) in length, while Stafford reports living worms as extending to 127. mm. (5 inches), a truly prodigious length. Stafford gives a normal length of 75 mm. Both Leidy and Stafford give the oral sucker as slightly larger than the acetabulum. Odhner (1911b) expresses the view that this trematode should be considered as a large *Azygia* species. Cooper (1915) collecting material from *L. masquinongy* considers his form the same as that reported by Stafford and identifies it as *Azygia lucii*.



Study of Leidy's original *Distomum longum* and Cooper's material clearly shows that they represent members of the genus *Azygia*. Their large size is certainly not sufficient basis to warrant Stafford in forming a genus, *Megadistomum*. Leidy's *Dist. tereticolle* (from *Esox reticulatus*) also was compared with them, and in the single specimen available in the Leidy collection, the oral sucker, contrary to Leidy's description, was found to be slightly larger than the acetabulum. In *Dist. longum*, Leidy describes the genital opening as "just anterior to the middle of the neck, or nearer the oral acetabulum." Such was not the condition in the two specimens of this form available. In each case the genital aperture was close in front of the ventral sucker, as is, indeed, characteristic of the genus *Azygia*. In the most elongate specimen the esophagus was unusually extended longitudinally and at its base a swollen region showed a marked resemblance to the cirrus sac. It is possible that Leidy mistook this appearance for the end-apparatus of the genital system. The true position of the terminal genital-apparatus in *Dist. longum* is seen in Figure 30.

Cooper also collected *Azygia* species from the pike (*L. lucius*). These latter trematodes were much smaller in size, and apparently a different species, but Cooper, after a careful comparison of his smallest examples from the maskinonge with those from the pike, concludes that they represent a single species. He also points out the highly variable size at which egg production begins. A 14. mm. trematode showed less mature eggs than one 6. mm. long from the same host. "On the other hand," Cooper adds, "examples of intervening lengths may have their uteri distended with ripe eggs!" (Cooper 1915:192). Forms from the trout were all immature although they reached a length of 11 mm.

This variable size at which eggs are first produced in *Azygia* species is in contrast with the fairly constant size at sexual maturity in *Otodistomum* species. The large number of different hosts in which *Azygia* species occur may be associated with this variability. Another possible factor is the season of the year, but the influence of this factor would be difficult to determine. Eleven different fish hosts have been reported for the present *Azygia* species. Ward collected his material in July and August and found that those forms from the smelt although attaining a length up to 11 mm., were always immature. Cooper does not indicate the season of his collection but found all forms from the trout and from the small-mouthed black bass immature. Stafford examined his fresh water fish in the spring and fall. One specimen of his "*Megadistomum longum*" measured 18. mm. long but contained no eggs; and the largest individuals of his "*A. tereticolle*" were smaller than immature individuals of *Megadistomum*. He found that most of his "*Mimodistomum angusticaudum*" were immature, but "towards the end of October" found a few sexually mature.

Whatever effect the season of collection may have, it is certain that what is evidently the same *Azygia* species does not attain sexual maturity at the same time in the different hosts in which it occurs. Thus, while average sized forms are producing eggs in such hosts as pike, pickerel, and salmon, specimens fully as large are still immature in such hosts as smelt, trout, small-mouthed black bass, and perch.

That variation in body size at sexual maturity may occur within a single host is shown by Cooper's report of a 14 mm. trematode with less mature eggs than were commonly found in specimens 6 to 14 mm. in length. Further data is needed, however, to show the extent of this variation. It has not been noted by other workers, and certainly is not so conspicuous as the marked differences found in specimens from different hosts.

The maximum body size which the trematode attains also seems associated with the host. In those cases wherein the greatest size is reached (as in the maskinonge and pike) there also seems to be considerable growth before sexual maturity (e.g. Stafford's immature 18 mm. specimen), and it is very possible that the ultimate size which the trematode may reach is associated with the amount of growth before eggs are produced, and this latter condition may, in turn, depend upon the fish host.

The following tables (Tables 10-13) show absolute measurements on these different forms. The 66 mm. specimen of *Dist. longum* was very highly extended and had apparently been stretched in killing. Moreover, the body was not equally extended but was more elongate in the uterus region just posterior to the acetabulum. The 37 mm. specimen therefore probably furnishes the more normal proportions.

TABLE 10. *Azygia seabago*  
Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
5.9	0.9	0.65	0.59	2.	1.4	0.31	2.12	0.72	0.72
5.9	0.9	0.65	0.59	2.	1.4	0.31	2.12	0.72	0.72
10.	0.93	0.65	0.58	4.37	1.9	0.65	2.75	2.	2.
6.7	1.06	0.65	0.56	2.25	1.5	0.41	2.18	1.31	1.18
11.5	0.75	0.67	0.56	4.06	2.	0.5	3.75	2.3	2.4
13.	0.5	0.74	0.56	5.3	2.5	0.9	3.25	1.9	1.9
9.	1.5	0.68	0.62	2.9	1.8	0.4	2.8	1.12	0.55
12.	1.1	0.8	0.5	4.8	3.	2.12	3.43	1.9	1.9
10.	0.81	0.71	0.52	4.18	2.56	1.3	3.18	1.93	2.28
10.5	0.81	0.65	0.56	3.6	2.4	1.06	3.37	2.12	1.87

TABLE 11. *Azygia bulbosa*  
Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
5.68	1.	0.81	0.62	2.43	1.68	0.65	1.49	0.75	0.75
6.3	1.37	0.87	0.62	2.2	1.8	0.65	1.5	0.75	0.75
6.2	1.25	0.81	0.68	2.4	2.1	0.58	1.6	0.7	0.7
8.4	2.9	1.25	1.	2.6	2.5	0.84	2.5	1.32	1.25
3.9	0.9	0.66	0.54	1.25	1.5	0.37	0.78	0.28	0.28
5.6	0.9	0.69	0.54	2.	1.6	0.58	1.6	0.73	0.92
7.1	1.1	0.87	0.63	2.	2.5	0.69	2.1	1.2	1.2
5.1	1.	0.75	0.56	1.68	1.62	0.9	1.3	0.74	0.74
4.18	0.9	0.56	0.35	1.3	1.49	0.5	1.12	0.55	0.55
6.9	1.1	0.81	0.62	1.9	2.	0.8	2.3	1.43	1.43
5.9	1.1	0.75	0.63	1.9	1.8	1.56	1.6	0.85	0.85

TABLE 12. Cooper's *Azygia lucii* from *L. masquinongy*  
Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
29.	2.06	1.06	1.06	15.3	4.	4.8	6.87	3.27	4.07
29.	2.1	1.1	1.1	12.3	4.4	7.5	9.6	4.	6.1
39.	2.18	1.25	1.25	17.	4.3	8.2	9.	5.6	4.4
31.	1.8	1.	1.	14.	3.68	5.3	9.1	5.23	3.3
	2.3	1.25	1.37		5.12	9.7			
	1.87						8.4	6.22	5.9
	1.68						9.6	5.3	6.8
		1.18	1.18						
		0.87	0.87						
3.4	0.5	0.48	0.5						

The large size of *Dist. longum* and the form from the maskinonge seems at first to separate them from most of the other forms. Leidy's *Dist. tereticolle*, however, somewhat bridges the gap.

The equal size of the suckers in the form from the maskinonge is distinct in these tables, but Cooper himself reports the oral sucker as larger than the acetabulum. In *Dist. longum* which this form most closely resembles, the oral sucker is larger. Moreover, Ward reports occasional equality of sucker-size in *A. sebago*. In view of these facts, the apparently constant equality of the size of the suckers in the above form is probably a coincidence, and at any rate could not alone justify a new species.

TABLE 13. Cooper's *Azygia lucii* from the pike

Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
142	1.6	0.93	0.75	4.18	2.7	0.25	5.	2.8	2.5
14.	1.12	0.78	0.56	6.3	2.9	0.89	5.	2.7	2.3
8.	1.	0.5	0.43	3.75	1.8	0.48	1.75	0.75	0.68
11.	0.75	0.68	0.56	4.75	2.5	1.5	2.68	1.18	1.37
7.5	0.87	0.67	0.52	2.9	1.6	0.28	2.	0.9	0.87
8.5	0.68		0.5	3.4	1.8	0.43	1.4	0.8	0.8
12.	0.93	0.75	0.62	5.5	3.9	0.9	2.18	1.5	1.

Leidy's *Distomum tereticolle*

20.3	0.97	0.8	0.71	9.3	3.9	2.5	7.1	3.6	3.6
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*Distomum longum*

66.	1.56	1.42	1.3	38.	6.8	18.7	12.1	7.1	7.1
37.	1.56	1.37	1.18	19.7	5.68		9.	4.	4.

The egg size is larger in the larger forms, but intermediate sizes were found in some of the material from the pike as shown by the following measurements.

TABLE 14

Average egg sizes in American forms of *Azygia*

<i>Azygia sebago</i> .....	48 by 27 $\mu$
<i>Azygia bulbosa</i> .....	48 " 28
Leidy's <i>Distomum tereticolle</i> .....	45 " 28
<i>Distomum longum</i> .....	62 " 34
Cooper's <i>Azygia lucii</i> from maskinonge.....	63 " 33
Cooper's <i>Azygia lucii</i> from pike.....	51 " 28
Cooper's <i>Azygia lucii</i> from pike.....	56 " 28

Two measurements are given in the last case as one trematode from this collection showed larger eggs.

The following tables (Tables 15-18) show the ratios of body length to: (1) width, (2) "neck" region, (3) uterus region, and (4) distance between ventral sucker and most anterior vitellaria.

TABLE 15

PROPORTION OF BODY LENGTH TO WIDTH IN AZYGIA SPECIES  
 BODY LENGTH IN MILLIMETERS IS GIVEN IN PARENTHESES

<i>A. sebago</i>	<i>A. bulbosa</i>	<i>A. angusticauda</i>	<i>A. acuminata</i>
6.5 ( 5.9)	5.68 ( 5.68)	7.7 ( 5.25)	3.8 ( 6.8)
11.7 (10.5)	4.6 ( 6.3)	7.9 ( 4.9)	3.6 ( 6.5)
6.2 ( 6.7)	5. ( 6.2)		4.2 ( 6.3 )
11.8 (10. )	3. ( 8.4)		3.7 ( 7.5 )
15.3 (11.5)	4.3 ( 3.9)		4.7 ( 8. )
26. (13. )	6.2 ( 5.6)		4.5 (11.3 )
6. ( 9. )	6.5 ( 7.1)		4.3 (10.9 )
10.9 (12. )	5.1		7.5 ( 9.75)
12.3 (10. )	4.6 ( 4.1)		3.8 ( 9.68)
	5.3 ( 6.9)		6.3 ( 9.87)
	4.4 ( 5.9)		7.2 ( 9.37)
Cooper's <i>A. lucii</i> from pike	Cooper's <i>A. lucii</i> from maskinonge	<i>Dist. longum</i>	Leidy's <i>Dist. tereticolle</i>
8.7 (14. )	14.5 (29. )	42.2 (66. )	20.8 (20.3)
12. (14. )	14.5 (29. )	23.5 (37. )	
14.6 (11. )	17.8 (39. )		
8.6 ( 7.5)	6.8 ( 3.4)		
12.9 (12. )			
8. ( 8. )			

TABLE 16

PROPORTION OF THE TOTAL BODY LENGTH TO THE DISTANCE FROM VENTRAL  
 SUCKER TO ANTERIOR END IN AZYGIA SPECIES

Body length in millimeters is given in parentheses

<i>A. sebago</i>	<i>A. bulbosa</i>	<i>A. angusticauda</i>	<i>A. acuminata</i>
4.2 ( 5.9)	3.3 ( 5.6)	2. ( 5.25)	2.4 ( 8. )
5.2 (10. )	3.5 ( 6.3)	2. ( 4.9)	2.9 (11.3 )
4.4 ( 6.7)	3. ( 6.2)		2.8 (10.9 )
5.7 (11.5)	3.3 ( 8.4)		3.1 ( 9.75)
5.2 (13. )	2.6 ( 3.9)		2.6 ( 9.68)
5. ( 9. )	3.5 ( 5.6)		2.7 ( 9.87)
4. (12. )	3. ( 7.1)		2.7 ( 6.87)
3.9 (10. )	2.7 ( 4.1)		3.7 ( 6.56)
4. (10.5)	3.4 ( 6.9)		2.8 ( 6.3)
	3.3 ( 5.9)		2.7 ( 7.5 )
Cooper's <i>A. lucii</i> from pike	Cooper's <i>A. lucii</i> from maskinonge	<i>Dist. longum</i>	Leidy's <i>Dist. tereticolle</i>
5.2 (14. )	7.2 (29. )	9.7 (66. )	5.2 (20.3 )
4.8 (14. )	6.6 (29. )	6.7 (37. )	
4.4 ( 8. )	9. (39. )		
4.7 ( 7.5)	8.3 (31. )		
4.4 (11. )			
4.7 ( 8.5)			
4. (12. )			

TABLE 17

PROPORTION OF TOTAL BODY LENGTH TO LENGTH OF UTERUS REGION  
IN AZYGIA SPECIES

Body length in millimeters is given in parentheses

<i>A. sebago</i>	<i>A. bulbosa</i>	<i>A. angusticauda</i>	<i>A. acuminata</i>
2.9 ( 5.9 )	1.9 ( 5.68 )	2.8 ( 5.25 )	3.6 ( 6.87 )
2.2 (10. )	2.8 ( 6.3 )	2.9 ( 4.9 )	2.8 ( 6.56 )
2.9 ( 6.7 )	2.5 ( 6.2 )		3.1 ( 6.3 )
2.9 (11.5)	2.5 ( 8.4 )		2.8 ( 7.5 )
2.4 (13. )	2.3 ( 3.9 )		3. ( 8. )
3. (16. )	2.8 ( 5.6 )		3.2 (10.9 )
2.5 (12. )	3.5 ( 7.1 )		2.95 ( 9.75 )
2.3 (10. )	3. ( 5.1 )		3.2 ( 9.68 )
2.6 (10.5)	3.2 ( 4.18 )		2.7 ( 9.87 )
	3.6 ( 6.9 )		
	3. ( 5.9 )		
Cooper's <i>A. lucii</i> from pike	Cooper's <i>A. lucii</i> from maskinonge	<i>Dist. longum</i>	Leidy's <i>Dist. tereticolle</i>
3.3 (14. )	1.9 (29. )	1.7 (66. )	2.2 (20.3 )
2.2 (14. )	2.3 (29. )	1.8 (37. )	
2.1 ( 8. )	2.3 (39. )		
2.3 (11. )	2.2 (31. )		
2.6 ( 7.5 )			
2.5 ( 8.5 )			
2.2 (12. )			

TABLE 18

PROPORTIONS OF THE BODY LENGTH TO THE DISTANCE FROM VENTRAL SUCKER  
TO THE MOST ANTERIOR VITELLARIA IN AZYGIA SPECIES

Body length in millimeters is given in parentheses

<i>A. sebago</i>	<i>A. bulbosa</i>	<i>A. angusticauda</i>	<i>A. acuminata</i>
19. ( 5.9 )	8.7 ( 5.68 )	26.2 ( 5.25 )	20. ( 8. )
14.4 (13. )	9.7 ( 6.3 )	27.2 ( 4.9 )	17.3 (11.3 )
16.7 ( 6.7 )	10.6 ( 6.2 )		29.4 (10.9 )
22.5 ( 9.1 )	10. ( 8.4 )		19.5 ( 9.7 )
15.5 (12. )	9.6 ( 5.6 )		28.2 ( 9.8 )
5.6 (19. )	10.5 ( 3.9 )		3.2 ( 9.68 )
23. (11.5)	10.2 ( 7.1 )		complete ( 6.8 )
7.5 (10. )	5.7 ( 5.1 )		13.1 ( 6.56 )
9.9 (10.5)	8.3 ( 4.18 )		28.6 ( 8.87 )
	8.6 ( 6.9 )		12.5 ( 9.37 )
	10.5 ( 5.9 )		22. (11. )
			complete ( 6.3 )
			complete ( 7.5 )
Cooper's <i>A. lucii</i> from pike	Cooper's <i>A. lucii</i> from maskinonge	<i>Dist. longum</i>	Leidy's <i>Dist. tereticolle</i>
45. (14. )	6. (29. )	3.5 (66. )	8.1 (20.3 )
15.7 (14. )	3.8 (29. )		
16.6 ( 8. )	4.7 (39. )		
7.3 (11. )	5.8 (31. )		
26.7 ( 7.5 )			
19.7 ( 8.5 )			
13. (12. )			

The relative width of the body is seen to be quite variable. Differences can be explained by different degrees of contraction, and by growth changes. The closely related genus, *Otodistomum*, has been shown to increase greatly in length but very little in width with growth. This condition is well shown by reference to the 39 mm. and the 3.4 mm. specimens (Table 12) from the maskinonge. In the former case the length is 17.8 times the width while in the latter the length is only 6.8 times the width.

*Dist. longum* and the form from the maskinonge have body lengths 7 to 9 times the neck regions, while in the other forms this ratio varies from about 3 to 5. But this difference is of no specific significance, being clearly due to the larger size of the former trematodes and representing a change in ratio which has been shown to occur with growth in similar forms. That is, the proportions shown in the table are what would be expected if all the forms represented different stages of growth of the same species. In the 66 mm. specimen of *Dist. longum* some allowance should perhaps be made for artificial extension which the other specimens did not receive.

The tables dealing with the uterus length and with the anterior extent of the vitellaria both indicate a slight tendency in *Dist. longum* to differ from the other species. In regard to uterus length, however, the smallest ratio (1.7) or longest uterus is in the specimen already described as showing a localized extension in that region. Furthermore, a tendency for this region normally to increase slightly its proportion to the remainder of the body was shown to be true in *Otodistomum*.

The anterior extent of the vitellaria is highly variable, as the body may be from 3.5 to 45 times the length of the distance between vitellaria and the acetabulum. Because of this high variation and because there is no consistency in any single group outside of *A. acuminata*, this point cannot be urged in separating species.

Thus, in spite of the great difference in size, a consideration of the possible features which might separate these species shows that there has been found no valid basis for distinction between them. It is especially significant that, except for characters which vary and overlap in the different forms, all the differences are in the direction taken by normal growth changes, and are moreover commensurable with such changes. Therefore, one feels justified in concluding that so far as can be determined morphologically, all these forms are representatives of the single species, *Azygia longa* (Leidy), and that this species manifests a variety of states, the extremes of which differ widely, but all of which are in accordance with growth changes and capacities known in related trematodes. The following fish are known hosts: *Salmo sebago*, *Osmerus mordax*, *Esox reticulatus*, *Anguilla chryspa*, *Perca flavescens*, *Esox lucius*, *Amiatus calvus*, *Esox masquinongy*, *Salvelinus namaycush*, *Lucioperca* sp., *Micropterus dolomieu*.

*AZYGIA ROBUSTA* ODHNER 1911

Odhner (1911b) established the species, *A. robusta*, "mit einer gewissen Reserve." This form (from the salmon) differs from *A. lucii* apparently in attaining a somewhat greater length (to 47 mm.) and in possessing a spherical although "mitunter etwas länger als breit" pharynx. The latter feature is the chief one upon which the species is founded. Odhner in his "ziemlich reichlichen Material" never finds the pharynx twice as long as wide, while in the material (*A. lucii*) from the pike, the pharynx is never spherical but always elongate. In a postscript, Odhner claims a substantiation of this new species on the character of the pharynx. As he gives no further specific differences between the new species and *A. lucii* it is to be inferred that the two are similar in other respects.

This distinction on pharynx shape introduces a new possible taxonomic factor for the group. The following measurements from favorable total mounts and cleared specimens might help in estimating the value of this character. The longitudinal axis of the pharynx is the first measurement given in each case. All measurements are in millimeters.

*Otodistomum cestoides*

0.54×0.39	0.48×0.39	0.37×0.24
0.56×0.37	0.71×0.56	0.35×0.26
0.46×0.41	0.54×0.50†	0.43×0.37
0.18×0.18*	0.50×0.29	0.37×0.37*
0.24×0.16	0.18×0.15	0.35×0.28
0.20×0.18†	0.56×0.39	0.56×0.46
0.18×0.16†	0.24×0.18	0.74×0.56
0.22×0.16	0.52×0.43	0.74×0.74*
0.18×0.15	0.46×0.35	0.44×0.31
0.46×0.37	0.37×0.29	

<i>A. sebago</i>	<i>A. bulbosa</i>	<i>A. acuminata</i>
0.35×0.20	0.31×0.31*	0.41×0.26
0.28×0.37*	0.20×0.22*	0.37×0.35†
0.18×0.11	0.37×0.41*	0.37×0.31
0.37×0.20	0.29×0.22	0.18×0.18*
0.46×0.28	0.29×0.28†	0.27×0.27*
0.28×0.18	0.41×0.41*	0.31×0.24
0.37×0.28		0.46×0.45†
0.28×0.22		
0.28×0.20		
0.20×0.14		



<i>A. loossii</i>	Cooper's <i>A. lucii</i>	<i>Dist. longum</i> Leidy
0.18×0.14	0.62×0.37	0.65×0.50
0.18×0.14	0.65×0.43	0.65×0.46
0.18×0.13	0.48×0.29	
	0.37×0.27	
	0.40×0.31	
	0.37×0.34†	
	0.32×0.27	

\* indicates that the pharynx is at least as wide as long.

† indicates that the pharynx is practically as wide as long.

A study of these figures shows that in no American species does the pharynx measure twice as long as wide; that it is ovoid rather than cylindrical; and that in all cases it may assume an almost spherical shape. For the European species, *A. lucii*, Looss (1894) describes the pharynx as cylindrical and his figure shows its length to be twice its width. Of this species Odhner (1911b:520) says: "Pharynx immer langgestreckt, etwa doppelt so lang wie breit, bei 18–22 mm. langen Exemplaren 0.6–0.8 mm. lang und 0.35–0.45 mm. breit." Accepting these records, there appears to be rather definite difference between *A. lucii* and all American species in the shape of the pharynx. Odhner's *A. robusta* resembles the American species in this respect. In view of the range of variability shown by the above measurements, this feature becomes of questionable specific value, particularly when considered alone. But until further comparisons with numerous specimens of European forms are made, the conclusions of Odhner will be accepted.

#### *AZYGIA PERRYII* FUJITA 1918

Fujita (1918) described this species from a fresh-water fish, *Hucho perryi* Breevoort, sent him by a friend. Fujita found the trematode attached to the external surface of the fish especially to the pectoral fin, oral cavity, buccal cavity, and outer and inner surfaces of the operculum and gills. This location of the parasite, although emphasized by Fujita, is, of course, of no significance since *Azygia* species normally inhabiting the anterior regions of the digestive system often migrate forward into the oral cavity and hence to the exterior. Such migration was noted as conspicuous in *A. sebago* by Ward (1910).

Fujita compares a few relative measurements of his form with *A. lucii* and *A. sebago*. His table of comparison follows. The figures are in percentages presumably based upon body length.

	A. perryii	Average	A. sebago	Average	A. lucii
Distance between oral and ventral suckers	18 19 17 18 18	18%	16 22 24 11 19	18%	24
Distance from anterior tip to center of ovary	54 53 47 50 49	51%*	54 56 54 63 66	59%	63
Center of ovary to center of post. testis	62 59 59 57 58	59%*	65 65 66 77 74	69%	74
Breadth behind ventral sucker	14 14 14 12 15	14%	16 21 17 6 19	16%	8

\* These two numbers are interchanged in the original table, but it is obvious that this is due to misprinting.

Fujita concludes from these figures that his species "has a resemblance to the American species in the distance between suckers and breadth of body, but in the location of the reproductive organs, which is very important, it is entirely different from the American species. On the other hand, the European species resembles closely the American species in position of reproductive organs, and on other points it differs from both American and Japanese forms." He does point out that these percentages are of comparative value only, since they will vary according to the methods used in preserving the specimens.

But Fujita's conclusions from his table are open to still more serious objections. The number of specimens compared is small as measurements of the single case of *A. lucii* were calculated from the figure by Looss (1894). Furthermore, all of the characters considered are influenced by different degrees of contraction and a contraction of any particular region of the body would alter such percentages. This fact might account for the high variation in the figures for *A. sebago*. But still more important, an analysis of the figures as they stand shows no valid differences between the three forms. The figures for *A. sebago* cover a range which includes figures for both the other forms in every character considered except "center of ovary to center of posterior testis" where 62% in *A. perryii* is the nearest approach to 65% in *A. sebago*. It is quite unexplained how "the position of the reproductive organs" in *A. perryii* is "entirely different" from the other two species. The derivation of the percentages in the character dealing with this distance from the ovary to the posterior testis is also not clear. The percentages (62% to 74%) certainly cannot be in relation to body length as the other figures appear to be, and 6.2% to 7.4% likewise are inappropriate for such ratio.

Two type specimens of *A. perryii* in the Ward Collection\* were available for study. Measurements of these specimens are as follows:

Length	8.6 mm.	5.6 mm.
Width	1.3	0.8
Oral sucker	0.78	0.58
Acetabulum	0.6	0.48
Post. edge acetab. to mid. ovary	2.	1.06
Post. edge acetab. to anterior end	2.18	1.8
Post. edge acetab. to most ant. vitellaria	right: 0.18 left: 0.56	0.09
Post. edge testis to post. end	3.1	1.9
Vit. on left beyond testis	0.74	0.84
Vit. on right beyond testis	0.2	*1.3
Pharynx	0.317 x 0.28	0.24 x 0.11

Fujita figures the vitellaria as terminating posteriorly in the immediate neighborhood of the posterior testis. I found that the posterior extent of the vitellaria was only slightly beyond the testis in the 8.6 mm. specimen, although they extended slightly over 1/2 the distance between this point and the posterior end on one side only in the 5.6 mm. specimen. In respect to this important point, Fujita says: "The posterior extent (of the vitellaria) extends somewhat farther down than the posterior testis" and adds that the vitellaria "do not extend posteriorly as far as in the American form." Since it has been seen that the vitellaria in *A. lucii* may extend some distance beyond the hind testis, it is apparent that *A. perryii* is like *A. lucii* and different from the American species in this respect.

Concerning the anterior extent of the vitellaria, Fujita says they reach "to near the posterior end of the ventral sucker," and concludes that this limit is further anterior than is reached by the European species. Looss describes them (in *A. lucii*) as failing to reach the acetabulum by a distance about equal to its diameter (his figure shows them ending posterior to such a point), and this is about their anterior extent as figured by van Beneden (1858). Although in the Japanese material they reach somewhat nearer

\* Collection of Dr. H. B. Ward, vial No. 18.83.

the acetabulum, the slight difference in this extent could not separate Fujita's form from the European.

Pharynx measurements of the two specimens in the above table showed one elongate pharynx and one ovoid. Fujita gives 0.29 by 0.2 mm.

Fujita's egg measurement was 0.058 by 0.033 mm. which is larger than the egg size in *A. sebago*, but about the size attained in the American form from the pike. Looss gives 0.045 by 0.023 mm. for *A. lucii*. Hence, in egg size the Japanese appears to differ from the European form, but that this distinction may not be a valid one has been indicated in the preceding comparison of American forms.

Fujita records the presence of the internal longitudinal muscles as described by Ward. He noted also that these muscles were located much more deeply (i.e., farther from the surface) on the dorsal side than on the ventral side. Thus, dorsally the cortical body region measured 0.21 mm., while on the ventral side this same region measured only 0.13 mm. in thickness. Such a condition was not true in American forms I studied. Leuckart's diagram of a cross-section of *A. lucii* is like *A. sebago* in respect to position of these muscles. Some variation in their position is probably accidental.

### *AZYGIA VOLGENSIS* (V. LINSTOW) ODHNER 1911

Synonyms: *Ptychogonimus volgensis* v. Linstow 1907

*Distomum volgensis* (v. Linstow) Lühe 1909

Odhner states that this species (from *Lucioperca sandra*) appears to be a true form. Apparently only very few specimens are known, v. Linstow studying only one. "Lühe's (1909) description is based on von Linstow's. Odhner (1911b) does not state the number or source of specimens he studied. His description is, however, very brief." It is certainly very close to *A. lucii* and no important distinction can be determined between the two from their descriptions. The length of *A. volgensis* is 5 mm. according to Odhner, and 6.2 mm. according to v. Linstow. Odhner contrasts "Eiproduktion" in *A. volgensis* at 2 mm. with this condition at 5 to 6 mm. in *A. lucii*, an entirely meaningless feature, in view of the variation the condition shows in American forms. These two European species should be further studied. On the basis of present evidence *A. volgensis* must be regarded as a doubtful species.

## SYNOPSIS OF THE GENUS AZYGIA

A key to the species of *Azygia* (including the several doubtful European species which might represent the single form, *A. lucii*) follows:

Vitellaria not extending appreciably posterior to the hind testis

Body length about 6 mm.; sexually mature at 2 mm. .... *A. volgensis* (v. Linst.)

Body length up to 30 mm. or more

Pharynx elongate, twice as long as wide; eggs 45 by 23 $\mu$  .... *A. lucii* (Muell.)

Pharynx globose; eggs? ..... *A. robusta* Odhner

Eggs 58 by 33 $\mu$  ..... *A. perryii* Fujita

Vitellaria extending considerably posterior to the hind testis, usually at least half way between this point and posterior end of body

Acetabulum near middle of body; gonads near posterior tip.. *A. angusticauda* (Staff.)

Acetabulum distinctly nearer the anterior end; gonads anterior from posterior tip by about 1/3 or 1/4 the body length

Body relatively wide; vitellaria beginning close behind acetabulum; neck usually constricted; internal parenchyma muscles weak; eggs about 64 by 33 $\mu$ ....

..... *A. acuminata* Goldberger

Body often extremely elongate; vitellaria usually beginning some distance posterior to acetabulum; internal parenchyma muscles strongly developed; eggs variable in size (up to 63 $\mu$  in length), usually about 48 to 55 $\mu$  by 28 to 30 $\mu$ .....

..... *A. longa* (Leidy)

## A GENERAL STUDY OF SOME MARINE FISH TREMATODES

Most of the following trematodes were collected at the Mount Desert Island Biological Laboratory during the summer of 1924. A brief account of these parasites has already been published (Manter 1925). The following descriptions give more complete data on them. A few trematodes from fish of the Woods Hole region are also considered. The study of these forms is based on specimens from the collection of Dr. Henry B. Ward. Extended descriptions are given only to those forms which are new or which have been briefly or incompletely described in the literature. Following the systematic arrangement adopted by Nicoll (1915) for trematodes of British fish, the forms studied would be grouped as follows:

- Order: DIGenea
- Sub-order: Prostomata
- Super-family: Distomata
- Family: Allocreadiidae
  - Sub-family: Allocreadiinae
    - Genus: Podocotyle
      - 1. *P. atomon*
      - 2. *P. olssoni*
  - Sub-family: Stephanochasminae
    - Genus: Stephanochasmus
      - 1. *S. baccatus*
  - Sub-family: Lepocreadiinae
    - Genus: Lepidapedon
      - 1. *L. rachion*
      - 2. *L. elongatum*
    - Genus: Homalometron
      - 1. *H. pallidum*
- Family: Zoogonidae
  - Sub-family: Lecithostaphylinae
    - Genus: Steganoderma
      - 1. *S. formosum*
- Family: Siphoderidae\*
  - Genus: Siphodera
    - 1. *S. vinalwardsii*
- Family: Azygiidae
  - Genus: Otodistomum
    - 1. *O. cestoides*
- Family: Hemiuridae
  - Sub-family: Hemiurinae
    - Genus: Hemiurus
      - 1. *H. levinseni*

\* Odnher may be correct in not recognizing this family.

- Sub-family: Sterrhurinae
  - Genus: Brachyphallus
    - 1. *B. crenatus*
- Sub-family: Lecithasterinae
  - Genus: Lecithaster
    - 1. *L. gibbosus*
  - Genus: Aponurus
    - 1. *A. sphaerolecithus*
- Sub-family: Syncoeliinae
  - Genus: Derogenes
    - 1. *D. varicus*
  - Genus: Genolinea
    - 1. *G. laticauda*
  - Genus: Gonocerca
    - 1. *G. phycidis*
- Sub-family: Accacoeliinae
  - Genus: Hirudinella
    - 1. *H. fusca*
- Unclassified genus: Deropristis
  - 1. *D. inflata*
- Order: MONOGENEA
  - Family: Tristomidae
    - Sub-family: Acanthocotylinae
      - Genus: Acanthocotyle
        - 1. *A. verrilli*
  - Family: Octocotylidae
    - Sub-family: Octocotylinae
      - Genus: Dactycotyle
        - 1. *D. minor*

## THE GENUS PODOCOTYLE

Stafford (1904) records "*Sinistroporus simplex* Rud." from seven different Canadian marine fish. He comments: "... genital pore to the left from the origin of the caeca in all specimens examined," and on this basis seems to found the new genus, *Sinistroporus*. The species is evidently the *Dist. simplex* Rud. that Linton describes from various fish of the Woods Hole region. The sinistral position of the genital pore is not sufficient, however, to separate the form from the genus *Allocreadium* in its older sense. Odhner (1905) considers *Dist. simplex* Rud. as probably synonymous with *Podocotyle atomon* (Rud.) and he also includes *Dist. simplex* Rud. of Levinsen (1881) as a synonym. Odhner redescribes the genus *Podocotyle* with *Dist. atomon* Rud. as type.

*Podocotyle*, originally a sub-genus of Dujardin's, was listed as a genus by Stossich in 1892. Stiles and Hassall (1898) established as type of this genus *Dist. angulatum* Duj. This species is, however, a species inquirenda, and Lühe (1900:491) remarks: Das endgültige Schicksal der Gattung ist demnach abhängig davon, dass diese Spec. inquir. einmal wieder gefunden

und dann auch wieder erkannt wird." According to Odhner (1905:321) this type material has been permanently lost, and the species is insufficiently described. He therefore assign: *Dist. atomon* Rud. as type species of *Podocotyle*. At any rate, the forms described as *Sinistroporus* are without doubt members of this genus as separated from *Allocreadium*. Such a synonymy is recognized by Nicoll in 1909 when he lists *Sinistroporus* Staff. as synonymous with *Podocotyle* (Duj.) Odhner. In an earlier paper Odhner (1901) had considered *Allocreadium atomon* (Rud.) as a highly variable species and recognized three varieties. In 1905, he determines *Podocotyle atomon* (Rud.) (= *Allocreadium atomon* (Rud.) Odhner 1901, e.p.) as a fixed species and his earlier varieties he considers as true species.

The diagnosis of the genus *Podocotyle* as given by Odhner (1905) is as follows: "Body elongate, quite evenly wide, sometimes flattened and ribbon-like, sometimes cylindrical. Esophagus at most twice as long as pharynx, forking in front of the ventral sucker. Genital pore to the left, lying at the level of the esophagus. Excretory vesicle reaching to the ovary. Cirrus-sac elongate, reaching at maximum as far as half way between ventral sucker and ovary. Seminal vesicle long, coiled. Pars prostatica lacking. Cirrus of marked length, straight. Ovary three-lobed. Vitellaria normally not reaching anterior to ventral sucker. Eggs without filament. In intestine of marine fish. Type species *P. atomon* (Rud.) Other species, *P. reflexa* (Crep.), *P. olssoni* Odhner (= *Dist. simplex* Olss. 1868 e.p.)."

Odhner refers to Linton's form as either identical with *P. olssoni* or closely related to it. Two species of *Podocotyle* were found in the present collection and these tend to confirm the constancy of the specific nature of the characters given by Odhner. In *P. atomon* the vitellaria are unbroken and do not come together between the testes; the testes are relatively small, not occupying over one half the cross-section of the body; the esophagus is longer than the pharynx; and the cirrus sac over-reaches the ventral sucker by a short distance. In both *P. reflexa* and *P. olssoni*, the vitellaria are broken near each testis and come together between these organs; and in both species also the testes are large, occupying a great part of the body in cross-section. *P. reflexa* differs in being cylindrical. It also has an esophagus longer than the pharynx. *P. olssoni* possesses and esophagus only as long or even shorter than the pharynx; and has a seminal vesicle reaching about half way between ventral sucker and ovary.

#### *PODOCOTYLE ATOMON* (RUDOLPHI 1802)

[Fig. 49]

From intestine, *Pholis gunnellus* (Butterfish)

From intestine, *Anarrhichas lupus* (Wolf fish)

One specimen of this species was taken from each of two butterfish of ten examined. These trematodes measured 2.37 mm. and 2 mm. in length.



Both of the specimens agreed in detail with Odhner's description of the species, with long esophagus, small testes, and unbroken vitellaria (Fig. 49). In one specimen the body was somewhat contracted and in this case the esophagus coiled somewhat instead of shortening with contraction, so that its length could be easily distinguished as about twice that of the pharynx. Cooper (1915) reports one young specimen of *Sinistroporus simplex* from the butterfish, but it is very probable that he was dealing with the same species now being considered. Both of the present specimens were fully mature.

The single specimen from the wolf-fish measured 3.06 mm. in length and 0.57 mm. in width. The esophagus was twice the pharynx length. The testes occupied about half the body width and were slightly lobed or crenulated as Cooper noted for *Sinistroporus simplex*. There was a slight break in the vitellaria opposite the hind testis, and the follicles approached each other between the testes. In these respects, the form showed a tendency to assume characters of *P. olssoni*, although these features are more marked in the latter species. In view of this possible variation of the vitellaria, the esophagus length seems to be the most useful distinction between the species.

*PODOCOTYLE OLSSONI* ODHNER 1905

[Fig. 50]

From intestine, *Urophycis tenuis* (Hake)

" " *Myxocephalus groenlandicus* (?) (Sculpin)

" " *Gadus callarias* (Cod)

" " *Microgadus tomcod*\* (Tomcod) Woods Hole

This trematode is a very common species. Fig. 50 shows the typical appearance of the material from the hake. The differences between this species and *P. atomon* have already been pointed out. The specimens from the hake show these differences most constantly and clearly. The esophagus is short (not longer than the pharynx); the seminal vesicle reaches to a point about half way between ventral sucker and ovary; the testes are large; and the rows of vitellaria are broken opposite each testis. The size was from 2.8 to 4 mm. in length by 0.4 to 0.58 mm. in width. The ventral sucker is prominent, usually somewhat protruded, and longer in its cross-diameter. It is almost exactly twice the size of the oral sucker. In one specimen the body wall about the sucker formed a slightly projecting fold around the sucker.

Material from the cod (which were of small size) agrees with the Woods Hole material from the tomcod. These forms show a few slight differences from the clear-cut specific characters of the form from the hake. The short

\* Collection of Dr. H. B. Ward, vial No. 13.75.

esophagus, however, is a constant character in which all agree. The breaks in the rows of vitellaria can usually, but not always, be discerned in the cod trematodes. The one or two cases wherein the follicles appeared continuous were of somewhat contracted specimens. The forms from the cod were all small in size. They measured 1.28 to 1.6 mm. by 0.26 to 0.3 mm. The seminal vesicle did not quite reach to a point half way between ventral sucker and ovary.

All of these forms also show two regions of slight body contraction, one about at the level of the posterior testis, the other usually slightly in front of the anterior testis. Figure 50 shows this condition only slightly evident. Sometimes it is conspicuous. Odhner does not mention it, nor does Linton, although the condition is shown in the figure of his *Dist. simplex* from the tomcod (Linton 1898, pl. 47, fig. 3). From Linton's description and figures there can be no doubt that his *Dist. simplex* (Linton 1898:525) is the same species as the present form from the tomcod. Linton records a length up to 2.4 mm., which approaches the size of the material from the hake. The egg size in all forms agrees, being 70 to 80 by 37 to 40 $\mu$ . Considering the above characteristic features, there can be little doubt that all the forms belong to the species, *P. olssoni*.

### STEPHANOCHASMUS BACCATUS NICOLL 1907

[Figs. 51-52]

From intestine, *Hippoglossus hippoglossus* (Halibut)

Five specimens of this trematode were obtained from the intestine of a single halibut. The largest specimen containing about 12 eggs measured 2.18 mm. in length. The smallest containing one imperfect egg was about 1.3 mm. in length. Measurements on the large specimen are as follows:

Length.....	2.187 mm.
Width.....	0.467
Oral sucker.....	0.176
Ventral sucker.....	0.256
Pre-pharynx.....	0.2
Pharynx.....	0.199 by 0.119
Eggs.....	85 to 91 by 45 to 51 $\mu$
Length of spines in posterior row.....	34 $\mu$
Length of spines in anterior row.....	28 $\mu$

In two specimens the number of spines in the oral ring was 29, but that this number may vary is shown by the fact that only about 25 spines were found in a third specimen. Nicoll found from 28 to 30 spines. The ring is unbroken, and the spines in the posterior ring are larger than those in the anterior ring.

The characteristic shape of the egg with one pole flattened was noted (Fig. 52). This condition at first seemed due to contraction, but Nicoll

reports it as specifically characteristic. In cross-section the eggs show a peculiar star-shaped outline (Fig. 52), which is evidently characteristic for all species in the genus.

### *LEPIDAPEDON RACHION* (COBBOLD) STAFFORD 1904

[Figs. 45-46]

Syn.: *Lepodora rachiaea* (Cobbold) Odhner 1905

From intestine, *Melanogrammus aeglefinus* (Haddock)

This trematode is fairly common and well known. Nicoll and Lebour each report it as common in the haddock of the English coast. Infection, however, is always light, usually only from one to three trematodes being found in a host. Its presence might accordingly be easily overlooked. In the present collection, two specimens were found from one host, and one each from two others. It is reported by Stafford (1904) from the same host. Stafford gives it the new generic name, *Lepidapedon* (for the form previously known as *Dist. rachion* Cobbold), but gives no description. Odhner (1905) gives a complete and carefully worked out description of the form which he named *Lepodora rachiaea* (Cobbold). In spite of the extent of Odhner's work, Stafford's name, *Lepidapedon*, holds priority and has been accepted by Nicoll and others. Stafford gives the measurement of 5 by 1 mm., but my specimens agree more nearly with those of Odhner who gives a length of 1.5 to 3.5 mm. with a width varying from 1/5 to 1/4 this measurement. The following measurements show general proportions:

Length.....	2.59 mm.
Width.....	0.46
Oral sucker.....	0.24
Ventral sucker.....	0.18
Pre-pharynx.....	0.285
Pharynx.....	0.19 by 0.17
X-diameter, ovary.....	0.11
X-diameter, ant. testis.....	0.17
X-diameter, post. testis.....	0.17
Length, sem. ves.....	0.285
Cirrus sac.....	159 by 114 $\mu$
Eggs.....	65 by 34 $\mu$

The morphology of the species is well known and the present material showed no new features. Most characteristic is the glandular mass of cells surrounding the seminal vesicle, and the location of the vitellaria ventral to the intestinal ceca.

Two other species of this genus have been described. Leiper and Atkinson (1915) describe a trematode which they name *Lepodora garrardi*. The corrected name would be *Lepidapedon garrardi* (Leip. and Atkin.). The description is not complete in regard to some points and indicates

(as the figure also shows) that their form approaches the genus *Lepocreadium* which it resembles in body shape and shortened pre-pharynx. No mention is made of any glandular cells surrounding the seminal vesicle.

Odhner mentions one other species but does not describe it. Miss Lebour in 1908 names a species *Lepodora elongata* (= *Lepidapedon elongatum* (Lebour)), and this species she suggests might be the form mentioned by Odhner. It differs from *L. rachion* by being more elongate in form, possessing a long esophagus, and with somewhat less extensive vitellaria. Several specimens, agreeing in most of these points are found in the present collection and were referred to this species.

### *LEPIDAPEDON ELONGATUM* (LEBOUR 1908)

[Figs. 47-48]

Syn.: *Lepodora elongata* Lebour 1908

From intestine, *Urophycis tenuis* (Hake)

Five specimens were collected from one out of three fish examined. The trematode shows close resemblance to *L. rachion* in general form, shape, arrangement of organs, and spiny cuticula, but differs from it in the length of the esophagus, extent and position of the vitellaria, and development of the glandular cells about the seminal vesicle. Also, the genital pore in this species is closer to the ventral sucker than in *L. rachion*. These same differences separate Miss Lebour's *Lepodora elongata* from *L. rachion*. The present form differs only in not being more elongate than *L. rachion*, but this point is one which may be influenced by age of the parasite or by body contraction. Typical measurements are as follows:

Length.....	2.4 mm.
Width.....	0.54
Oral sucker.....	0.119
Ventral sucker.....	0.14
Pre-pharynx.....	0.125
Pharynx.....	0.09
Esophagus.....	0.091
X-diameter, ovary.....	0.29
X-diameter, ant. testis.....	0.31
X-diameter, post. testis.....	0.37

Miss Lebour does not record the position of the vitellaria in relation to the ceca. As has been noted, in *L. rachion* the vitellaria are ventral to the ceca. In the present form, this condition did not hold but the vitellaria were found distributed on both sides of the intestine. They extend anteriorly at least to the ventral sucker in *L. rachion*, but fail to reach the level of this sucker in *L. elongatum*. Another conspicuous difference between the two species is found in the character of the glandular mass surrounding the seminal vesicle. The cells in this mass are large, globular,

and numerous in *L. rachion* (Fig. 46), but are much reduced in *L. elongatum* where they are very inconspicuous (Fig. 47). In this respect, *L. elongatum* approaches the related genus *Lepocreadium*. My material also resembles Miss Lebour's and differs from *L. rachion* in that the testes are separated from each other by a distinct space. The pharynx is considerably smaller than in *L. rachion*.

### *HOMALOMETRON PALLIDUM* STAFFORD 1904

[Figs. 54-56]

From intestine, *Fundulus heteroclitus*

This species is the same form referred to by Linton (1901:422, pl. 32, Fig. 354) and named *Homalometron pallidum* by Stafford in 1904. Stafford does not describe the genus or species, merely referring to Linton's paper. Linton's description is as follows:

"Body very minutely spinose, white translucent; acetabulum and oral sucker about the same size; outline of body, long oval; neck short, continuous with body; greatest breadth in region of testes, near posterior end; ecaudate; acetabulum sessile; rami of intestines simple, elongate; esophagus as long as pharynx; testes two, in median line behind uterus; seminal vesicle dorsal to ovary and posterior border of acetabulum; ovary between acetabulum and testes, on right side; pharynx sub-globular; genital aperture in front of acetabulum, on median line; vitelline glands lying at posterior end and along sides of body as far as acetabulum; ova, few, relatively large. Dimensions of specimen in formalin, given in millimeters: Length 2.72; breadth, anterior 0.43, at acetabulum 0.89; middle 1.07, near posterior end 0.36; diameter of oral sucker 0.26; diameter of acetabulum 0.29; diameter of ovary 0.21; diameter of testes 0.33 and 0.39; ova 0.11 and 0.07 in the two principle diameters."

Looss (1907:613-14) criticizes Stafford for establishing a genus without description. As Looss shows, the trematode seems to agree with the genus *Lepocreadium* Stoss. This genus was established in 1903, or prior to Stafford's *Homalometron*.

The genus *Lepocreadium* contains the following species: *L. album* (Stoss.), *L. pegorchis* (Stoss.), *L. trulla* (Lint.) and *L. levinseni* (Lint.). Odhner (1905) erects a new sub-family of the Allocreadiidae, *Lepocreadiinae*, for this genus and *Lepidapedon* (= *Lepodora*). In a later paper (1914) Odhner identifies the cercaria of *Lepocreadium album*, the type species, and gives an account of the morphology of the adult. As is common, some of the most distinctive characters of the genus are found in the distal male genital apparatus.

The present form is strikingly like the genus *Lepocreadium*. It shows similar size, form, spiny cuticula, suckers, digestive system, excretory

system, vitellaria, and position of the gonads. So far as the description of Linton shows, the form could easily belong to this genus, the chief point of difference being the median location of the genital pore instead of a position to the left, as in *Lepocreadium*. This pore was clearly median also in my material.

The most important features were found in the male reproductive apparatus. In *Lepocreadium* a prominent cirrus sac is present. It encloses the prostate gland and an anterior region of the seminal vesicle, which is thus divided into two parts. In the form from *Fundulus*, however, the cirrus sac is entirely absent. The seminal vesicle is globular and swollen in form and is not divided into two regions (Fig. 55). It opens directly into the pars prostatica, the glandular cells of which lie free in the parenchyma at about the level of the ventral sucker. The prostate gland is poorly developed. The vagina seems to join the male duct shortly beyond the prostate gland and there is a long genital sinus. The absence of a cirrus sac would seem to be of generic significance and, in fact, together with the median genital pore, violates the sub-family diagnosis. Other features of the trematode are so similar to *Lepocreadium* that it must be considered a very closely related genus.

The seminal receptacle is large and located close behind the seminal vesicle, as in *Lepocreadium*. A short Laurer's canal is present. No spines could be detected in the cirrus or vagina. The yolk reservoir is large and located posterior to the ovary. The eggs are very large. A specimen with only two eggs showed them to be fully as large or even larger than the ovary. The spiny or scaly cuticula layer is very evanescent as has been noted for *Lepocreadium*, and may be lost in preserved material. It is most conspicuous on the dorsal anterior regions and thins out in the tail region. The glandular mass about the posterior tip of the excretory vesicle is present as in *Lepocreadium*.

Very young forms of this distome were sometimes found in large numbers embedded in the intestinal folds of the host. Moreover, from the stomach of the fish cysts were found which clearly contained this trematode as shown by the finely spined cuticula of the cercariae within the cysts. As the *Fundulus* had been in salt water aquaria for some time, the indication is that infection is derived from marine rather than from fresh water sources. In spite of the fact that immature specimens were sometimes found in large numbers, infection with the adult form was never heavy, and many uninfected fish were found. Usually not more than two or three specimens were taken from one host.

*STEGANODERMA FORMOSUM* STAFFORD 1904

[Figs. 58-60]

From pyloric ceca, *Hippoglossus hippoglossus* (Halibut)

Six specimens of this interesting trematode were obtained from the ceca of a single halibut. The only description of the form seems to be by Stafford who also found it in the ceca and intestine of the halibut.

The taxonomic position of this trematode is very close to the genus *Lecithostaphylus* Odhner 1911 (Odhner 1911a) which it markedly resembles, but from which it differs in certain distinct characters. The genus *Lecithostaphylus* is placed by Odhner in the family Zoogonidae, and, indeed, is used as a basis for a new sub-family, *Lecithostaphylinae*. Including the present genus, the family contains the following genera:

Family: Zoogonidae

Sub-family: *Lecithostaphylinae*Genus: *Lecithostaphylus**Stegano-**derma**Proctophantastes**Lepidophyllum*

Sub-family: Zoogoninae

Genus: *Diphterostomum**Zoogonoides**Zoonogenus**Zoogonus*

Odhner places *Lecithostaphylus* "an die Spitze der Familie" and from this genus assumes that the entire family might be derived from the, *Fellodistominae* (*Steringophorinae* of Odhner\*) with which it agrees in genital and digestive systems. In the *Fellodistomidae*, the cirrus is short and wide, a condition occurring also in *Lecithostaphylus* but differing from its elongate form in the remaining genera of the Zoogonidae. *Stegano-*  
*derma* combines the elongate cirrus with marked similarities to *Lecithostaphylus*, and hence represents a step between the latter and other genera of the sub-family.

An outline of the genus based on Stafford's description with some additions might be as follows: Body elongate, regular in outline, flattened, both ends regularly rounded, anterior end slightly broader. Scale-like spines covering body to near the posterior end. Suckers about equal in size, ventral sucker a little more than 1/3 from the anterior end. Very small pharynx, long esophagus, ceca extending slightly more than half the body length. Ovary median or to one side, just posterior to the ventral sucker. Testes side by side at ends of ceca. Uterus between testes and filling posterior body. Cirrus sac somewhat elongate, almost straight,

\* Nicoll (1913) is correct in pointing out that Odhner is not justified in changing *Fellodistominae* Nicoll to *Steringophorinae*.

reaching posteriorly to and sometimes overlapping the ventral sucker, crossing left cecum between ventral sucker and the forking of the intestine. Genital opening ventral and to the left about half way between cecum and margin of body. Vitellaria lateral, reaching only from ventral sucker to the testes, composed of a few large follicles. Laurer's canal present. Type species: *S. formosum* Stafford.

This genus is like *Lecithostaphylus* Odhn. in body shape, size, spiny cuticula, intestine, gonads, vitellaria, and uterus; but differs from it in possessing a very small pharynx, long esophagus, elongate cirrus, well developed excretory bladder, and Laurer's canal with pore.

The following measurements are from an average sized specimen:

Length.....	3.25 mm.
Width.....	0.86
Thickness.....	0.2 to 0.28
Oral sucker.....	0.224
Ventral sucker.....	0.24
Diameter of ovary.....	0.26
Diameter of testes.....	0.355
Pharynx.....	97 by 68 $\mu$
Esophagus.....	0.285
Eggs.....	34 by 17 $\mu$

There is no pre-pharynx. The posterior end of the esophagus splits into two short branches each about 46 $\mu$  long. That is, the intestine proper does not begin at the point of bifurcation, but the esophagus histologically extends slightly beyond this point.

The excretory system is simple, expanded tube-like in form, and extends from the posterior tip almost to the posterior border of the ventral sucker where it spreads out laterally, T-like. It lies mostly dorsal to the uterus. Near its anterior end it becomes so swollen as to fill the larger part of a cross-section of the body in that region. It here comes in close contact with the intestinal ceca from which it is separated by a very narrow distance (Fig. 59). An excretory duct at the posterior tip of the vesicle is lined by a cuticula-like layer continuous with the external body cuticula. In the parenchyma about this duct appear what seem to be gland cells, pyriform in shape and with large nuclei (Fig. 60).

Within the parenchyma, in the anterior body region, especially in the vicinity of the esophagus, numerous, conspicuous, round to oval bodies occur. They are without nuclei and their content is very finely granular and homogeneous. They exhibit a very strong affinity for eosin stain, which colors them immediately and tenaciously. These bodies which almost fill the parenchyma anteriorly thin out posteriorly, and disappear at about the level of the ventral sucker. Their size varies, being about 13 to 39 $\mu$  in longest diameter. The nature and function of these bodies could not be determined. They were not found in any other trematode



of the present collection. The cells in the neck region of *Siphodera* described by Linton (1911) differ markedly from these bodies in appearance. In *Siphodera*, the cells have definite nuclei.

The position of the ovary is just posterior to the ventral sucker, but it may be either median or slightly to one side. The ootype is small, without membrane, and lies posterior to the ovary. Laurer's canal is present, is only slightly coiled, and opens dorsally just posterior to the ovary. A seminal receptacle seems to be absent. The uterus leads posteriorly, coiling between the testes, filling the hind body, and returning to course ventrally over the ovary. The vagina begins at about the level of the ventral sucker, leads anteriorly and obliquely to the left parallel with the cirrus sac, to which it is at first lateral on the left and then dorsal. The male duct joins the vagina ventrally and there is a common genital sinus for a short distance about  $60\mu$ .

The number of follicles in the vitellaria is fairly but not exactly constant. It is sometimes difficult to determine the exact number, as some follicles are seen to be double in nature, an indication of an evolutionary change either toward a more compact or a more diffuse condition of these organs. Eight or nine follicles were found on the right side and ten to twelve on the left.

The two ducts from the testes arise from the anterior aspects of these organs and course anteriorly lateral to the excretory vesicle and between this organ and the ceca. The ducts unite just posterior to the termination of the excretory vesicle, and continue forward for some distance as a single duct in the mid-body region. At about the level of the anterior border of the ventral sucker this duct enters the muscular cirrus sac and becomes the seminal vesicle. This vesicle is poorly developed. It is scarcely, if any, coiled. A slight constriction separates it from the well-developed pars prostatica which, surrounded by gland cells, occupies most of the cirrus sac. The ejaculatory duct is unarmed. In the 3.25 mm. specimen the cirrus sac measured about 0.69 mm. in length and 0.19 mm. in width at its widest point. The seminal vesicle extended about 0.176 mm., the pars prostatica 0.34 mm., and the ejaculatory duct 0.17 mm.

### THE HEMIURIDAE

The Hemiuridae include many of the most common marine trematodes. Typical members of the family are those forms with a "tail appendage" such as *Hemiurus*, *Brachyphallus*, and *Dinurus*. Lühe founded the family in 1901, and included in it also such forms as *Derogenes* and *Accacoelium*. Looss (1907a) later limited the conception of the family, excluding the two latter genera. Odhner (1911b) points out that *Derogenes* is so closely related to the other Hemiuridae that separation from that family is impossible. The inclusion of *Derogenes* necessitates the adoption of

Genarches and other Syncoeliinae. Odhner also included the Accacoeliinae and the *Hirudinella clavata* group. Nicoll reviews the status of the family and agrees with Odhner in accepting its broader conception according to which "Looss's Hemiuridae takes the position of a sub-family" (Nicoll 1913:245). Nicoll also extends the boundaries of the family slightly to include his genera, Hemipera and Derogenoides. The family has thus become so broad as to be very difficult to describe. At present, it must be considered as a large variable group, containing (Nicoll 1915) the following sub-families: Hemiurinae, Diurinae, Sterrhurinae, Lecithasterinae, Syncoeliinae, and Accacoeliinae. Considering *Hirudinella* as belonging in the last sub-family, members of each of these sub-families except Dinurinae have been met with in the present studies.

A few words should be said in respect to the use of the term "cirrus sac" in this group (Hemiuridae). In the Hemiuridae, the two sex ducts unite to form a more or less elongate tube-like "ductus hermaphroditus" or genital sinus which leads to the common genital pore. This condition of the terminal genital region in the Hemiruidae has been rather fully discussed in the literature. Pratt (1898) reviews the situation and gives its history to 1898. Levinsen (1881) and Juel (1889) termed the common terminal portion of the genital tract the genital vestibule. It is perhaps now more commonly known as the genital sinus. Pratt and Juel both believe that the terminal portion of this vestibule or genital sinus has arisen as "an invagination of the body wall and is homologous to the genital cloaca of other trematodes." Juel believes that the remainder of the duct represents the distal end of the uterus which has come to serve as a genital sinus by the dropping back of the ejaculatory duct. Pratt, however, believes that it has been the uterus that has dropped back and hence that most of the sinus is homologous with the forward end of the ejaculatory duct.

Whatever its origin, it is known that this genital sinus can function as a cirrus, and is protrusible. Looss noted such a functioning in 1896 for *Apolema mollissimum*. Because the genital sinus functioned as a true cirrus, the muscular sac surrounding it he considered as a true cirrus sac. He says (p. 125): "Or, en ne tenant compte que de ses rapports avec le canal renfermé, je crois déjà pouvoir la considérer avec raison comme une véritable poche du cirrhe: ces fonctions viennent parfaitement à l'appui de cette interprétation." In the same discussion, however, Looss himself notes that the term is not strictly correct. Thus, in regard to "la poche du cirrhe," he says (p. 127): "... "à proprement parler ce terme n'est pas tout à fait exact; mais connaissant maintenant ses rapports avec le reste des organes génitaux, nous pouvons nous en servir pour plus de simplicité." Other authors (e.g., Lühe 1901, Lander 1904, Odhner 1905,

Lebour 1908) agree in calling the muscular sac around the genital sinus a true cirrus sac.

Strictly speaking, it does not seem appropriate to refer to this structure as a true cirrus sac. The cirrus is a definite organ belonging strictly to the male genital system. The genital sinus in Hemiuridae, although functioning as a cirrus and although probably homologous with the cirrus, cannot be termed a true cirrus, since it is a duct common to both male and female systems. It has never been referred to as a cirrus, but as the "genital sinus" or "ductus hermaphroditus." To call the sac surrounding it a cirrus sac is then a misnomer. Since this structure surrounds the genital sinus, it seems more appropriate to refer to it as a sinus sac. This sinus sac in Hemiuridae certainly functions as a cirrus sac, and is probably homologous with the cirrus sac. The difference is, however, a distinct one. For the expression of the association of the sac with a common sex duct instead of with the male duct alone, it is felt that the term "sinus sac" is justified. It has already been used by the present author in an earlier paper (Manter 1925). Some such term seems all the more advisable in view of the fact that in Nicoll's genus *Hemipera* a true cirrus sac appears to be present, containing "not only the ductus ejaculatorius but also the pars prostatica" (Nicoll 1913:245).

### *HEMIURUS LEVINSENI* ODHNER 1905

[Figs. 62-63]

From stomach, *Gadus callarias* (Cod)

From stomach, *Urophycis chuss* (Squirrel hake)

Species of the genus *Hemiurus* are among the most common trematodes of marine fish. Distinction between species is, however, rather difficult. Looss in 1907 perhaps drew the most careful lines between species. It has been customary, especially previous to 1907, to refer most specimens which are clearly *Hemiurus* to the species *appendiculatus*. Thus, Stafford (1904) lists *H. appendiculatus* from ten different fish of Canadian waters. His only comment is: "Suckers of equal size." Looss shows that true *H. appendiculatus* up to 1907 had probably been found only in *Alosa finta*. He adds the additional hosts, *Gadus eurusinus* and *Mugil capito*, in the latter of which the parasite might be accidental.

The following are some of the most distinctive characters of *H. appendiculatus* as given by Looss: Ventral sucker about twice as large as oral sucker; ring of the cuticula disappearing dorsally at about the level of the pharynx; cirrus sac elongate, reaching a length about  $\frac{3}{4}$  the diameter of the ventral sucker; anterior part of the seminal vesicle very muscular; coils of uterus can stretch relatively far into the tail appendage, and come near the ends of the ceca.

All of the material collected from the Mount Desert Island region and belonging to the genus *Hemiurus* apparently belongs to the species, *H. levinsoni*. The almost equal size of the suckers, with the oral sucker slightly larger is a constant character and one which separates the species from *H. appendiculatus*, *H. communis*, *H. lukei*, and *H. rugosus*. Since all of Stafford's representatives of this genus collected from Canadian fish show this character, it is very probable that they should belong in this species rather than in *H. appendiculatus*. Odhner reports *H. levinsoni* from *Gadus morrhua* f. *ovak*, *Cottus scorpius*, and "many northern fish." It seems to be the most common *Hemiurus* species in arctic marine fish. In temperate waters the other species showing larger ventral suckers and small oral suckers are common. Thus, Linton's *Dist. appendiculatum* from Woods Hole fish shows a sucker proportion of about 1 : 2.

*Hemiurus levinsoni* also differs from *H. appendiculatus* in possessing a shorter prostate tube, in a more constantly retracted tail appendage into which the uterus does not commonly extend, and in the cuticular rings extending dorsally to the level of the ovary.

In the present material, as in Odhner's, the tail was almost always completely retracted. The ceca may enter the tail slightly. In a single specimen the tail was fully extended and in this case both the ceca and a portion of the uterus extended into it (Fig. 62). The genital pore is median just behind the mouth opening. The genital sinus is long, and in contracted specimens the prostate tube does not begin until about the level of the ventral sucker. This tube is long and more or less curved according to body contraction. The seminal vesicle is large and divided into two sections, the anterior of which is surrounded by a muscular coat. The sizes of the specimens vary from 0.7 mm. to 1.68 mm. in length. Eggs measurements of 23 to 26 by 10 to 13 $\mu$  agree well with Odhner's measurements of 26 to 28 by 12 to 13 $\mu$ .

Eighteen specimens were taken altogether from the stomachs of six squirrel hake examined. Eight specimens were collected from three cod.

Cooper (1915) reports this species encysted in the muscles of small herring.

Measurements on four typical specimens are as follows:

Length.....	1.68 mm.	1.12 mm.	1.06 mm.	0.99 mm.
Width.....	0.467	0.37	0.374	0.37
Oral sucker.....	0.176	0.176	0.142	0.159
Ventral sucker.....	0.188	0.17	0.136	0.142
Pharynx.....	91 by 91 $\mu$	91 by 74 $\mu$	68 by 62 $\mu$	85 by 74 $\mu$
Eggs.....	23 12 $\mu$	23 13 $\mu$		26 10-13 $\mu$

*BRACHYPHALLUS CRENATUS* (RUDOLPHI 1802)

[Fig. 53]

From stomach and intestine,	<i>Osmerus mordax</i>	(smelt)
" " " "	<i>Pollachius virens</i>	(Pollack)
" " " "	<i>Clupea harengus</i>	(Herring)

Lander (1904) has described the morphology of this form in detail. His material was also obtained from the smelt. In the present collection thirteen specimens were obtained from the stomachs and intestines of three smelt. Two other fish examined did not contain the trematode. The worms usually occur in the stomach.

Looss (1907:158) expresses the view that the American form of this parasite represents a new species which he names *B. affinis*. He finds the chief distinction to be the elongate and less lobed condition of the vitellaria and that the host and geographical occurrence differ widely from the European *B. crenatus* from *Salmo salar*. Lander figures the vitellaria as about twice as long as wide in an extended specimen, and his description indicates that this is the usual condition. In regard to lobation of these organs, Lander says: "They are commonly slightly lobulated, though they sometimes have a regular oval outline." Cooper (1915) describes and figures one specimen from a small herring. This specimen agreed with *B. crenatus* in having definitely lobed vitellaria (right, four lobed; left, three lobed). He also points out that either gland may appear entire when viewed obliquely. He suggests that the herring may represent an intermediate host and that the trematode might be discovered in *Salmo salar* from America.

The present material from the smelt agrees with descriptions of *B. crenatus* (Rud.). It is probably the same species collected by Lander from the same host. The vitellaria, however, in my specimens from the smelt were always distinctly lobed (Fig. 53), usually one being four-lobed, the other three-lobed. In none of the specimens were the vitellaria noticeably longer than wide. On the basis of these thirteen specimens from the smelt, it would appear that the American species is not distinguishable from the European species, *B. crenatus*. For hosts of *Brachyphallus crenatus* Odhner gives: *Cottus scorpius*, *Pleuronectes limanda*, *Gasterosteus aculeatus*, *Ammodytes tobianus*, *Salmo salar* and *trutta*, and *Osmerus eperlanus*. Lander's material was from *Osmerus mordax* and *Anguilla chrysypa*.

The smelt from which the present material was collected occurred in large numbers, together with small cod and pollack beneath the fishing wharf at Manset. All these fish were about the same size and evidently had similar feeding habits. The same trematode, *Brachyphallus crenatus*, was obtained from the stomach of the pollack, *Pollachius virens*, but not from the cod. Specimens from the pollack agreed in every respect with

those from the smelt. They were relatively small and usually contracted. The vitellaria were constantly lobed. Four fish yielded eleven trematodes.

Eight or nine specimens were obtained from the examination of 28 herring (*Clupea harengus*). The much larger size of most of these trematodes gave the impression of a different species, but the details of anatomy agreed with *Brachyphallus crenatus*. Moreover, the sizes agree with known limits for the species (Odhner recording a variation of 0.8 mm. to 2.5 mm. in body length, while Olsson gives 5 mm. as maximum length). Cooper (1915) found one small specimen in the stomach of the herring. The present collection of large mature specimens from this host indicates that the herring is a normal host for the parasite and not, at least exclusively, an intermediate host as suggested by Cooper.

Only in material from the herring was variation in vitellaria shape noted. In these specimens, lobing of the vitellaria was not common. The characteristic four- and three-lobed condition was clearly evident, however, in one specimen. The material from the herring agrees in this respect with Lander's description, although an elongate condition of the vitellaria was not common.

### *LECITHASTER GIBBOSUS* (RUDOLPHI 1802)

[Fig. 61]

From intestine, *Myoxocephalus octodecimspinosus* (?), Sculpin

Looss (1907) gives the following synonyms for this species:

*Distomum mollissimum* Lev. 1881<sup>1</sup>  
nec *Distomum mollissimum* Stoss. 1889  
nec *Apolema mollissimum* Lss. 1896

Odhner (1905) reports this species from various northern fish (including *Cottus scorpius*). He separates the species from *Lecithaster confusus* Odhner. This latter species has the following synonymy:

*Apolema mollissimum* Lss. 1896  
nec *Distomum mollissimum* Lev. 1881  
*Hemiurus bothryophorus* Lss. 1899  
nec *Distomum botryophoron*<sup>2</sup> Olss. 1868<sup>3</sup>

A single specimen was collected from the intestine of one fish out of eleven examined. Stafford (1904) reports a species as *Lecithaster bothryophorus* Olsson (= *Apolema mollissimum*) from the salmon and herring.

<sup>1</sup> This date printed 1891 was evidently a misprint.

<sup>2</sup> Olsson originally spelled this name *botryophoron*, but the word has been very commonly referred to as *bothryophoron*. Lühe (1901) called the species *Lecithaster bothryophoron* using it as type of the genus *Lecithaster*. Odhner (1905) shows this species to be actually *Lecithaster gibbosus* (Rud.).

<sup>3</sup> Given as 1869.

Odhner (1905) assigned *Lecithaster bothryophorus* as the type of a new genus *Lecithophyllum*. As *Apoblema mollissimum* is a synonym of *Lecithaster nfusus*, the actual identification of Stafford's material which is undescribed is unknown. Linton (1901 and 1905) reports *Dist. bothryophoron* from various fish, but to which species of *Lecithaster* his form belongs cannot be determined from his descriptions or figures.

The two species *Lec. confusus* and *Lec. gibbosus* are closely related. The present specimen was assigned to the latter species because of the thickness of the ovarian lobes, the length of the vitelline lobes, and because the seminal vesicle did not extend posterior to the ventral sucker. According to Looss, these three points are the chief means of distinction between the two species.

Measurements on the specimen are as follows:

Length.....	1.12 mm.
Width.....	0.4
Oral sucker.....	0.17
Ventral sucker.....	0.256
Pharynx.....	0.09 by 0.09
Eggs.....	23 to 26 by 15 $\mu$

#### *APONURUS SPHAEROLECITHUS* MANTER 1925

[Figs. 70-74]

From stomach, *Urophycis tenuis* (Hake)

The genus *Aponurus* is considered by Looss (1907) as most nearly related to *Lecithaster*, although showing relationships to *Brachyphallus*. The only other species in the genus is *A. laguncula* Lss.

The trematodes of this genus are small in size (about one millimeter in length) and almost cylindrical in form, tapering anteriorly but broadly rounded posteriorly. The ventral sucker, located about  $1/3$  from the anterior end, is almost exactly twice the size of the oral sucker. The genital pore is about at the level of the pharynx. The genital sinus is surrounded by a conspicuous pear-shaped sinus sac. Vagina or metraterm is lacking or very short. Seminal vesicle rather short, swollen, mostly anterior to the ventral sucker. Testes, ovary, and vitellaria globular. The vitellaria are in two groups, one of four, another of three follicles. They are more or less spherical, and are located just posterior to the ovary. Coils of the uterus fill the body posterior to the vitellaria, but anterior to the ovary are more limited to the space between the intestinal ceca.

The genus *Aponurus* bears close relationship to *Lecithaster* and *Lecithophyllum*. *Lecithophyllum* was created by Odhner (1905) for Olsson's *Distoma botryophoron*. Odhner studied Olsson's type material. The following table, showing differences between the three genera is based on data as given by Odhner and Looss.

<i>Lecithaster</i>	<i>Lecithophyllum</i>	<i>Aponurus</i>
(1) Genital pore rather distant from oral sucker	Genital pore rather close to oral sucker	Genital pore rather close to oral sucker
(2) Ovary 4-lobed	Ovary entire	Ovary entire
(3) Posterior end tapering	Posterior end broadly rounded	Posterior end broadly rounded
(4) Pars prostatica much longer than genital sinus	Pars prostatica shorter than genital sinus	Pars prostatic as long as genital sinus
(5) Genital sinus reaching about to ventral sucker	Genital sinus reaching almost to ventral sucker	Genital sinus reaching only about half way to ventral sucker
(6) Eggs small (15 to 25 $\mu$ ) thin-shelled	Eggs large (60 $\mu$ ) thick-shelled	Eggs small (26 $\mu$ )
(7) Vitellaria elongate in 7 connected parts	Vitellaria elongate in 7 connected parts	Vitellaria rounded in 7 separate parts

The significance to be attached to the distinctly separated nature of the follicles of the vitellaria might be questioned and perhaps should not be considered as of generic value. Looss himself brings up this question. In his discussion of *Lecithaster* he says (Looss 1907:161): "Einen gewissen Anklang an die bei den Verwandten herrschenden Verhältnisse kann man vielleicht darin erblicken, dass die 7 Schläuche nicht selten so gelagert sind, dass mehr oder weniger deutlich eine Gruppe von 4 und eine von 3 Schläuchen entsteht." Yet in *Lecithaster* and *Lecithophyllum* the follicles are described as distinctly united centrally. Again, Looss seems to express some doubt as to whether the vitellaria in *Aponurus* are all actually unconnected. He says (p. 168): "Bei der Pressung frischer Tiere geht die Kugel-form in eine Birn- oder Keulenform über, die Gruppen von 3 und 4 bleiben meist deutlich sichtbar, verschinden manchmal aber ebenfalls, und dann ähneln die Dotterstöcke vollkommen denen von *Lecithaster*, da die Schlauche alle von einem Punkt auszugehen scheinen. Ich glaube auch, dass dies tatsächlich der Fall ist, obwohl der direkte Nachweis an ganzen und aufgehellten Individuen wegen der ungünstigen Lagerung der Follikel nicht zu erbringen ist." Yet, if it be true that the vitellaria are actually as in *Lecithaster* then there is much less justification for separation of *Aponurus* from *Lecithophyllum*. The condition of the vitellaria in the present material will be discussed below.

Two specimens of this form were obtained from the stomach of one fish. These specimens agree in the main with the characters of the genus. Both seemed fully mature and their size measurements were 1.47 by 0.29 mm., and 1.1 by 0.245 mm. The greatest thickness is about the same as the greatest width, so that at the ventral sucker and posterior the worm is cylindrical. The body is broadly rounded at the posterior end. The cuticula is smooth and there is no tail appendage. The sucker proportion is almost exactly 1 : 2. Pre-pharynx lacking, pharynx globular; esophagus short; wide ceca reaching to the posterior end of the body.



The excretory system is as in other Hemiurids. Posteriorly it is concealed by egg masses. The unpaired vesicle branches between the ovary and testes, and the two lateral branches unite dorsal to the pharynx.

The genital pore is ventral, median, at about the level of the middle of the pharynx. The pear-shaped muscular sinus-sac extends dorsally and posteriorly from the pore and surrounds the genital sinus. It reaches about half way to the ventral sucker. In this posterior extent of the genital sinus the form differs from *Lecithophyllum*. The wall of the sac consists of an outer layer of longitudinal muscles and an inner layer of circular muscles. Between these layers and the sex duct is a space filled by parenchyma tissue containing a few cells. The width of this parenchyma-filled space is about equal to the combined thickness of the muscle layers. The common genital duct coils somewhat within the sac, at the posterior end of which it splits into the male and female sex ducts.

The testes are located a short distance posterior to the ventral sucker. In both specimens the right testis was slightly anterior to the left. Their size is relatively small, and in this respect they differ from the condition in *A. laguncula*, where the testes fill a large portion of the body cross-section. The seminal vesicle is large, and ovoid or simple-sac like in shape. In *A. laguncula* it is bent slightly at each end. In the present species it extends posteriorly to near the middle of the ventral sucker. In *A. laguncula*, it does not extend very far beyond the anterior margin of the sucker.

The duct of the pars prostatica leads from the ventral surface of the seminal vesicle near its anterior end, bends directly dorsally over the anterior end of the vesicle, reaches to the dorsal wall, and then bends again ventrally to unite immediately with the uterus to form the genital sinus. The wall of the duct is composed of small flat cells apparently without ciliary processes. The form of the pars prostatica is S-shaped in lateral view (Fig. 70), and the gland does not run directly posteriorly as in *A. laguncula*. The cells of the prostate gland are large in size and somewhat angular in shape. The total length of the gland is just about equal to the length of the sinus sac. Thus, in length it agrees with *A. laguncula* and differs from *Lecithophyllum botryophoron*. In a 2 mm. specimen of the latter species, the genital sinus was 0.3 mm. long and the pars prostatica 0.17 mm. or about 1/2 as long. In the 1.1 mm. specimen of *A. sphaerolecithus* the pars prostatica was about 0.19 mm. in length. In this same specimen the sinus sac was about 0.2 mm. in length measured from the lateral aspect. This proportional length is about as in *Lecithophyllum*, but due to the dorsal slant of the organ its posterior edge only reached a point about half way to the ventral sucker.

The ovary is located a short distance posterior to the testes and slightly to the right. It is spherical in form and smooth in outline. The globular

seminal vesicle is located anterior and slightly dorsal to the ovary. It is about one half the size of the ovary. Laurer's canal is absent.

The vitellaria consist of seven follicles, globular in shape a smooth with outline, and located close together just posterior to the ovary. They are in two groups. One group of four is located to the right and just posterior to the ovary, while the group of three is located to the left (Figs. 73-74). The follicles in the group of four are larger, being almost as large as the ovary. This size of the follicles is greater than in *A. laguncula*, where they are about one half the size of the ovary. The position of both ovary and vitellaria is near the ventral surface of the body. In regard to the separate or connected condition of the follicles, a series of sections through the larger specimen gave no indication that the follicles are united at any point. While some were in close contact with each other, others were clearly isolated. In spite of Looss's question, this condition seems definitely distinct, certainly from the normal condition in *Lecithaster* and from the condition described for *Lecithophyllum*. More material will be necessary to settle the point finally.

The coils of the uterus are as in *A. laguncula*. The terminal region of the uterus is surrounded by the cells of the prostate gland. The uterus runs close to the male duct in this region and with it swings dorsally over the anterior end of the seminal vesicle (Fig. 72). The male and female ducts do not unite outside the sinus sac. The male duct opens into the extreme posterior tip of the sac, while the female duct enters from the left at practically the same spot.

The eggs are very large and this character forms a conspicuous difference between the two species of *Aponurus*. Looss gives the eggs of *A. laguncula* as about 0.027 mm. in length and 0.016 mm. in width. Eggs in the present species were 0.056 to 0.065 mm. by about 0.026 mm. This size and the thick egg shell agree with *Lecithophyllum*.

Measurements are as follows:

Length.....	1.47 mm.	1.1 mm.
Width.....	0.296	0.245
Oral sucker.....	0.137	0.1
Ventral sucker.....	0.264	0.19
Ant. end to post. edge ventral sucker....	0.617	0.43
Pharynx.....	63 by 63 $\mu$	57 by 57 $\mu$
Diameter, ant. testis.....	68 $\mu$	57 $\mu$
Diameter, post. testis.....	79 $\mu$	68 $\mu$
Diameter, ovary.....	91 $\mu$	85 $\mu$
Diameter, vitellaria.....	85 to 91 $\mu$	62 to 72 $\mu$
Eggs.....	58-62 by 26 $\mu$	56-65 by 26 $\mu$

*GENOLINEA LATICAUDA* MANTER 1925

[Figs. 64-66]

From stomach, *Hippoglossus hippoglossus* (Halibut)

Small to medium-sized forms, with flattened body tapering slightly anteriorly, at which end it is roundly pointed; body broadly rounded posteriorly. Body almost uniformly wide. Cuticula smooth. Tail appendage lacking. Oral sucker embedded in body, overlapped dorsally by fleshy lip. Ventral sucker about one and a half times the size of the oral sucker, located anterior to the middle of the body and about at the end of the first body third. No pre-pharynx, pharynx broad, esophagus very short, ceca broad, extending to posterior tip of body. Excretory system as in Hemiuridae, branches uniting dorsal to pharynx. Genital pore median, ventral, at about the level of the forking of the intestine. Testes compact, globular, obliquely behind one another some distance behind the ventral sucker. Ovary large, compact, globular, located behind testes. Vitellaria behind one another posterior to ovary, compact, globular. Uterus sends two lateral coils posterior to vitellaria to near body tip. Between ovary and ventral sucker the uterus is in large transverse coils. Genital sinus short, seminal vesicle much coiled, just anterior or slightly overlapping the ventral sucker. Eggs 28 to 31 by 12 to 15 $\mu$ .

The Hemiurid affinities of this form are seen in the digestive and excretory systems, the general form, shape, and position of the gonads, the genital sinus, prostate gland, and oral lip. It is most closely related to *Genarches* Lss. and *Derogenes* Lühe. which are grouped under the Syncoelinae. It differs from both in body shape which is not markedly tapering at either end, and in position and proportional size of the ventral sucker which is distinctly anterior to mid-body. None of the three specimens showed contraction of the neck region, so that this sucker position can be assumed as normal. The course of the uterus in *Genolinea* is distinctly different than it is in either *Genarches* or *Derogenes*. *Genarches* is, of course, also clearly separated by the union of the two intestinal ceca posteriorly.

*Genolinea*, in addition to points already mentioned, is distinct from *Derogenes* in possessing a very short prostate gland, a much coiled seminal vesicle, and a more linear arrangement of the reproductive organs.

Measurements on two of the specimens are as follows:

Length.....	1.87 mm.	1.32 mm.
Width.....	0.336	0.299
Oral sucker.....	0.136	0.125
Ventral sucker.....	0.239	0.199
Ant. end to post. edge ventral sucker....	0.617	0.5
Pharynx.....	57 by 79 $\mu$	57 by 74 $\mu$
Ant. testis.....	0.136 mm.	0.1 mm.

Post. testis.....	0.136	0.13
Ovary.....	0.165	0.15
Ant. vitellarium.....	0.114	0.12
Post. vitellarium.....	0.142	0.12
Eggs.....	31 by 13 to 15 $\mu$ 28 to 31 by 12 $\mu$	

### *GONOCERCA PHYCIDIS* MANTER 1925

[Figs. 67-69]

From gills and branchial cavity, *Urophycis chuss* (Squirrel Hake)

Body elongate, both ends bluntly rounded, cuticula smooth, not ringed, body only slightly flattened, oval in cross-section, tail appendage lacking. Ventral sucker posterior to middle of body, almost twice as large as the oral sucker, about as wide as body. Mouth opening sub-terminal, overlapped dorsally by lip-like projection of body, oral sucker embedded in body. No pre-pharynx, short esophagus, intestinal ceca reaching to posterior end of body. Excretory vesicle branching just posterior to the ovary, the branches running forward laterally and uniting dorsal to the oral sucker near the anterior tip. Gonads crowded together posterior to the ventral sucker and filling most of the body space in that region. Genital aperture median and ventral, close behind mouth opening. Ovary median just behind ventral sucker, anterior to the testes. Vitellaria compact, unlobed, lateral and very slightly posterior to the ovary. Testes large, just posterior to the ovary, obliquely behind and in contact with each other. Ootype without membrane, dorsal and anterior to the ovary. Eggs comparatively large. Seminal vesicle comma-shaped, pointed anteriorly, located at about the level of the pharynx. Prostate gland little developed, free, short, located ventral to the oral sucker just anterior to the seminal vesicle. The covering of the seminal vesicle seems to be non-muscular, hence the cirrus sac is absent or at most weakly developed. There is a short genital sinus. No localized seminal receptacle. Region of the uterus just anterior to the ovary often crowded with sperm cells.

About 15 specimens were taken from the gills and branchial cavity of a single host. The fish had been caught but a few hours and it is possible that (as is true of some other Hemiurids) the gill region is the normal habitat of the parasite. Two specimens altogether, however, were obtained from the stomach of this fish.

That this trematode belongs to the non-appendiculate Hemiuridae there can be no doubt. Its features characteristic of the family are seen in the excretory system, projection of upper lip, position of genital pore, and character and form of the gonads. It differs from most members of the family in the reversed position of the ovary in relation to the testes. Still more marked distinctions are found in the location of the uterus entirely anterior to the ovary, in the position of the seminal vesicle far

distant from the ventral sucker, in the position of the prostate gland, and in the crowded localization of the gonads and vitellaria in the tail region.

The occurrence of the parasite on the gills and in the branchial cavity of the host is not unique among the Hemiuridae. Odhner gives the following as "gill parasites": *Accacoelium contortum*, *Syncoelium*, *Otiotrema*, *Bathycotyle*, and *Liocerca*. Of these forms, the present species resembles most closely *Liocerca*. *Liocerca* is also one of the few members of the family with testes posterior to the ovary. *Gonocerca* differs markedly, however, from *Liocerca* in the following points: position of the genital pore, which is considerably more posterior in *Liocerca*; position of the seminal vesicle, which is close to the ventral sucker in *Liocerca*; length of the prostate gland, which is elongate in *Liocerca*; and in uterine coils, which extend posterior to the ovary in *Liocerca*. *Liocerca* shows more resemblance to *Hemiurus* than does *Gonocerca*.

Nicoll in 1913 describes the genus *Hemipera* which he considers most closely related to *Liocerca*. It resembles this genus in inverted position of the ovary. In this respect, it is also like the present form with which it shows further similarity in position of the ventral sucker. The body form of all three genera is very similar. In *Hemipera*, the testes are lateral to each other, instead of behind one another, as in the other two genera. *Hemipera* shows the widest divergence in possessing a cirrus sac inclosing both prostate gland and seminal vesicle, and in having egg with polar filaments.

A tabular comparison of these genera follows:

	<i>Liocerca</i>	<i>Gonocerca</i>	<i>Hemipera</i>
Habitat	gills	gills	stomach
Position of genital pore	Somewhat distant from oral sucker	Close to oral sucker	Somewhat distant from oral sucker
Position of ventral sucker	About mid-body	Posterior to mid-body	Posterior to mid-body
Testes	Behind one another	Behind one another	Lateral to each other
Cirrus sac	Inclosing only male duct	Absent	Inclosing prostate gland and sem. ves.
Prostate gland	Free, elongate	Free, short	Inclosed
Seminal vesicle	Near ventral sucker	Near pharynx	Between suckers
Eggs	Numerous, non-filamented	Numerous, non-filamented	Few, filamented

Form, shape, size, cuticula, excretory and digestive systems are similar in all three genera.

*Gonocerca* differs from *Derogenes* in extent and position of prostate gland, position of genital pore, course of uterus, and inverted position of ovary in relation to testes. These same differences except extent of prostate gland separate it from *Genarches*.

Measurements on five specimens are as follows:

Length.....	1.8 mm.	1.9 mm.	1.3 mm.	1.4 mm.	1.4 mm.
Width.....	0.48	0.37	0.29	0.37	0.4
Ant. end to post. border					
ventral sucker.....	1.3	1.3	0.89	1.	1.
Oral sucker.....	0.26	0.22	0.18	0.2	0.22
Ventral sucker.....	0.43	0.37	0.29	0.33	0.35
Ovary.....	0.2	0.12	0.13	0.12	0.125
Testes.....	0.22	0.19	0.17	0.23	0.23
Vitellaria.....	0.15	0.1	0.1	0.114	0.114
Pharynx.....	114 by 85 $\mu$	80 by 80 $\mu$	74 by 85 $\mu$	96 by 51 $\mu$	85 by 79 $\mu$
Eggs.....		46 to 50 by 20 to 26 $\mu$			

### *DEROGENES VARICUS* (MÜLLER 1784)

[Fig. 57]

From Stomach, *Gadus callarias* (Cod)

" " *Urophycis tenuis* (Hake)

" " *Urophycis chuss* (Squirrel hake)

" " *Anarrhichas lupus* (Wolf fish)

Intestine, *Hippoglossus hippoglossus* (Halibut)

" *Myxocephalus octodecimspinosus* (Sculpin)

This parasite is known as perhaps the most common marine fish trematode. It shows a very extensive host range, although usually present in small numbers. Nicoll reports mature specimens as small as one millimeter in length while Stossich gives a maximum length of 7 mm. The parasite is quite easily distinguished from other Hemiurids by its lack of tail appendage, position of ventral sucker posterior to middle of the body, small terminal sinus sac inclosing both sex ducts, its long prostate, and large eggs. There is no pre-pharynx. The genital opening is about at the level of the branching of the intestine. Gonads are similar to those of the typical Hemiurids. Measurements on an average sized specimen from the cod were:

Length.....	1.7 mm.
Width.....	0.5
Oral sucker.....	0.22
Ventral sucker.....	0.37
Ovary.....	0.14 x-diameter
Testes.....	0.14 x-diameter
Pharynx.....	85 $\times$ 85 $\mu$
Eggs.....	50 $\times$ 28-30 $\mu$

Stafford (1904) names a new species *Derogenes plenus* briefly described from the wolf fish. The single specimen from that host in the present collection showed no specific difference from *D. varicus* and there appeared no justification for assigning it to a different species. Whether or not it represents Stafford's form is, of course, unknown; but in view of the meager description of *D. plenus* the species seems somewhat uncertain.

*HIRUDINELLA FUSCA\** (POIRIER 1885)

[Figs. 75-79]

Synonyms: *Dist. fuscum* Poir.*Dist. verrucosum* Poir.*Dist. clavatum* of LintonFrom Stomach, *Xyphias gladius* (Sword fish) Woods Hole

This trematode belongs to the interesting group of large forms represented by *Dist. clavatum*. Considering the early discovery and long history of trematodes of this group, precise knowledge of their internal structure is rather meager. The history and synonymy of the group has been given by Poirier (1885), Buttel-Reepen (1903), and Mühlschlag (1914) and will not be discussed here. The group itself is well isolated (although referred to by Odhner as representing a sub-family of the Hemiuridae), yet the species within it are remarkably similar. The early custom of dependence on external features has led to confusion and uncertainty of species. Poirier's work (1885), while dealing in detail with the morphology of the group, does not bring out clear distinction between species. The later work of Buttel-Reepen and Mühlschlag has separated with considerable definiteness the following species which evidently should all be referred to the genus *Hirudinella*: *Dist. clavatum*, *Dist. ampullaceum*, *Dist. seimersi*, *Dist. fuscum*, and *Dist. ingens*. The *Dist. insigne* of Poirier is a synonym of *Otodistomum veliporum*, and his *Dist. verrucosum* is considered by Mühlschlag as identical with *Dist. fuscum*.

In his various papers from Woods Hole, Linton records *Dist. clavatum* from the stomach of *Xyphias gladius*. He describes the form to some extent in his 1896 paper. Cooper (1915) identifies as *Hirudinella clavata* trematodes collected from the stomach of *Thunnus thynnus* in Canadian waters. The present material from *Xyphias gladius* at Woods Hole is very probably the same form recorded by Linton. Since Linton's description is incomplete and since the more recent work of Mühlschlag emphasizes new specific characters in the genus, a brief description of this form might be of some importance.

One vial of the material contained 60 specimens varying from 7 to 23 mm. in length and from 2.5 to 5 mm. in width. The body is very robust, stout, thick, and very cylindrical especially posterior to the ventral sucker. The posterior end is broadly rounded. The neck region is smaller than the swollen hindbody, and in a 23 mm. specimen measured about 6 mm. in length. The body is marked by transverse folds or wrinkles characteristic of the group and due to body contraction. The ventral sucker is very prominent with wide, sometimes wrinkled or corrugated margins. Its width is often greater than the width of the body (Figs. 76-77). In a

\* Collection of Dr. H. B. Ward, vials Nos. 13.44 and 13.45.

12 mm. specimen, the oral sucker was 1.17 mm. in diameter, the ventral sucker 2.19 mm., and the pharynx  $0.64 \times 0.42$  mm.

The extraordinarily thick body wall is made up of (1) a thick cuticula, (2) a "sub-cuticular" layer in which occur (especially in the neck region) circular and longitudinal muscle fibers, (3) a thick circular muscle layer, and (4) an inner layer of longitudinal muscles. Internal to this last layer there occurs a well-defined cellular layer which has been called the sub-cuticular cellular layer. The condition of these layers were found as reported by Mühlischlag. The circular layer is more prominent anteriorly. In the mid-body regions the longitudinal layer is enormously developed and the fibers are grouped into conspicuous bundles. This layer may represent the internal parenchyma muscles of *Otodistomum* and *Azygia*.

The oral sucker opens directly into the pharynx. There is a strongly developed esophagus which, in contracted specimens, leads dorsally and anteriorly from the posterior end of the pharynx. The esophagus splits before losing its cuticular lining, and the lumen of each branch expands into a roomy tube. These two esophageal expansions open into the anterior regions of the intestinal ceca. Here the ceca are modified into swollen, bulb-like regions characterized by cells with extremely long, cilia-like processes which practically fill the wide lumen. These modified regions have been called glandular. They lead abruptly into the ceca proper which are lined with small cells having short, cilia-like processes. The ceca stretch to the posterior end of the body, and become very large in regions posterior to the ventral sucker, filling the greater part of the large body of the worm. Considerable amount of black food substance occurs within the intestinal ceca.

Excretory vessels permeate all regions of the parenchyma, so that almost any section through the trematode shows cross-sections of numerous tubes of this system. There is an unpaired excretory vesicle extending as a laterally flattened tube between the two enormous ceca. This vesicle opens to the exterior through a short duct provided with circular, longitudinal, and oblique muscles. The plexus of accessory excretory tubes is very complicated. The unpaired vesicle divides into two branches just behind the posterior limit of the uterus and vitellaria, or about half way between the posterior and anterior ends of the body. The lateral branches evidently wind and bend extensively, and the accompanying plexus of various sized vessels continue into the region of the oral sucker.

The genital pore is median, ventral, and nearer the oral sucker (Linton gives its position as mid-way between the suckers). In material of the present studies it occurred about opposite the posterior end of the pharynx. It leads into a very large genital atrium which is somewhat flattened parallel with the ventral body surface (Fig. 75). The genital opening is near the anterior limit of this atrium. A conspicuous genital papilla



projects into the atrium from its dorsal surface and on the truncated tip of this papilla the male sex duct opens. The vagina does not enter the papilla. Its opening is posterior to this papilla and separated from it by a depression in the atrium wall. This widely separated position of the openings of the sex ducts into the atrium is characteristic for *H. fusca* and Figure 75 shows almost exact agreement with Mühlschlag's diagram of that region. In *H. clavata*, the two ducts open close together on a common papilla (Poirier 1885).

The testes lie obliquely behind one another close behind the ventral sucker which they may slightly overlap dorsally. The somewhat coiled seminal vesicle leads into the duct of the large prostate gland. The prostate gland is lined with cells bearing cilia-like processes. The prostate gland coils slightly. At the base of the genital papilla the duct changes abruptly into the ejaculatory duct. This duct possesses a very thick inner coat of cuticula, and a powerful layer of circular muscles. It is, moreover, provided with numerous muscles which attach themselves to its outer wall. These muscles run obliquely through the papilla, and dorsal to it some of them are seen to lead anteriorly to the longitudinal body muscles of the dorsal side. Others, leading posteriorly, split off from the longitudinal muscles of the uterus. Still others seem to be connected with longitudinal body muscles of the ventral and lateral sides (Fig. 79).

In *Dist. ingens* and *Dist. ampullaceum* where the two ducts open in common, special musculature surrounds not only the ejaculatory duct but also the terminal region of the vagina. This common muscular system surrounding both ducts was called a cirrus sac by Buttel-Reepen (1903), but that it could not be correctly interpreted as such was pointed out by Mühlschlag who called it the "genital musculature." This condition of both sex ducts being surrounded by a common musculature brings to mind the so-called "cirrus sac" about the genital sinus in some Hemiuroids. Homologies would be difficult to draw, however, since the genital sinus in the latter case is probably a composite of the true genital atrium and the fused sex ducts.

The ovary is located just posterior to the testes. The ootype lies in contact with it posteriorly and ventrally. Both organs are surrounded by a fibrous membrane some of the fibres of which seem to bind the two together as in *Otodistomum*. The left vitelline duct runs between the ootype and ovary to unite with the right duct somewhat to the right of the middle line. The common vitelline duct penetrates the ootype anteriorly. It unites with the oviduct within the ootype. Laurer's canal also penetrates the membrane of the ootype. It enters more toward the posterior, although likewise from between ovary and ootype. This canal is very powerfully developed with a cuticular lining and a thick wall of circular muscles. It is unusually long, since the ootype is near the ventral

surface and the canal opens to the exterior dorsally at about the level of the ovary. After its penetration into the ootype, it opens into a swollen, bulb-like enlargement which lacks the muscular coat. This swollen region in turn leads into a narrow duct which opens into the oviduct slightly before the vitelline duct (Fig. 78). The thin-walled enlargement of Laurer's canal seems to be morphologically a true seminal receptacle. No spermatozoa, however, were seen anywhere along the length of the canal.

The uterus coils posteriorly between the intestinal ceca to a point about half way between anterior and posterior ends of the worm. It then coils anteriorly, extending dorsal to the ovary and testes, ventral to the seminal vesicle, and opening into the atrium as already indicated. At about the level of the ovary the character of its wall changes and includes circular and longitudinal muscle layers, and, outside the latter, a dense layer of small coils of supposedly glandular function. Overhanging, lip-like folds of the atrium about the opening of the vagina may serve as a valve to prevent re-entrance of eggs into the vagina from the atrium which is often well filled with them. Furthermore, out-pocketings of the vagina close to its tip results in forming a second valve-like fold within the vagina itself (Fig. 79). The constancy of this structure is, however, unknown.

The vitellaria are tubular and winding. They occur laterally on each side of the body. Anteriorly they reach to about the level of the testes, and posteriorly as far as the posterior extent of the uterus. The rather thin-shelled eggs are broadly ovoid and measure about 32 by 25 $\mu$ .

From the morphological features discussed above, it is evident that the species must be referred to *H. fusca*. Most characteristic is the nature of the genital atrium. Mühlenschlag gives also the following specific characters: the short, thick-set body form; the swollen borders of the ventral sucker; and the bulb-like swelling of Laurer's canal within the ootype.

### *SIPHODERA VINALEDWARDSII*\* (LINTON 1899)

[Figs. 80-83]

From *Opsanus tau* (Toad fish), Woods Hole

Synonym: *Monostomum vinaledwardsii* Lint. 1899

This form was first named and imperfectly described as *Monostomum vinaledwardsii*. This original material was obtained by Linton, also from the toad-fish at Woods Hole. In 1911 Linton found further material of the same species from *Ocyurus chrysurus* at Tortugas. He corrects and extends his former (1899) description and places the form in a new genus (Siphodera) of the distomes. This genus with a few other genera from the same region (Tortugas) he includes in the new family Siphoderidae.

The present form agrees very largely with Linton's later description. As he was, however, uncertain in regard to some points, the form will be briefly described here.

\*Collection of Dr. H. B. Ward, vials no 22.217, 22.218.

The body shape is broadly oval in outline and somewhat pointed at each end. It is somewhat flattened but is thicker in the middle regions. An average sized specimen measured 1.88 mm. in length, 1.33 mm. in width, and 0.53 mm. in greatest thickness, which was through the region of the ventral sucker. The body surface is covered with minute scale-like spines. The circular oral sucker is at the anterior end. In regard to the ventral sucker, Linton (1911) says: "The ventral sucker is a part of the genital apparatus (cirrus) and is depressed in a circular pit of the body wall. The border of the pit is muscular and has strong muscular fibers radiating from it." This description applies to the position of the ventral sucker, the bordered pit and radiating muscles being conspicuous even in toto-mounts, but the sucker itself has no direct connection with the genital system. The common opening of the sex ducts is just anterior to the sucker and just within the border of the pit (Fig. 83), as will be shown later. The sucker is therefore referred to in this paper as the ventral sucker instead of using Linton's term "genital sucker." This sucker is smaller than the oral sucker, and is located a little less than  $\frac{1}{3}$  the body length from the anterior end. In a 1.8 mm. specimen the oral sucker measured 0.2 mm. in diameter and this ventral sucker only 0.09 mm. The diameter of the genital pit (which incloses both the genital pore and the ventral sucker) was 0.16 mm. The ventral sucker may be protruded from the pit (Fig. 82). There is a short pre-pharynx, globular pharynx, and short swollen esophagus. The intestinal ceca are widespread and reach almost but not quite to the posterior tip of the body.

The excretory system is very simple. The unpaired excretory vesicle occupies a large part of the central region of the hind-body. It opens at the posterior end through a short duct which is surrounded by deeply staining cells. Just posterior to the ovary or not far behind the ventral sucker, the vesicle splits into two lateral branches which continue forward and end blindly beside the oral sucker. They occur internal to the intestinal ceca, cross them ventrally in the region of the esophagus, and run on each side of the pharynx.

The musculature of the body wall is poorly developed. There is a weak circular layer and a longitudinal layer of somewhat separated bundles. The powerful diagonal muscle bands which run out obliquely and laterally from the border of the genital pit seem to originate in the neighborhood of the longitudinal body muscles. The ventral sucker is provided with two strong muscles which are attached to its outer border laterally and lead almost directly dorsally to the region of the seminal vesicle (Fig. 82). The body parenchyma is very loose and open.

The testes are in two groups in the lateral regions of the middle of the body. The number is variable, usually 4 or 5 on each side. They are located near the dorsal surface, so that ventrally they are considerably

concealed by the egg-filled coils of the uterus. The seminal vesicle is median in position, anterior to the testes, with its anterior limit over-reaching the posterior border of the ventral sucker. It is swollen tube-like in form and slightly coiled. Its walls are quite thick and evidently muscular, although the direction of the fibers could not be made out. At about the level of the ventral sucker it bends ventrally and is constricted off (by an inward continuation of its wall) from a succeeding bulb-like portion (Fig. 83). This latter region leads ventrally tapering, carrot-like. Its outer wall is also heavy like that of the seminal vesicle. The distal portion represents the ejaculatory duct. A short distance before it reaches the genital pore, it is joined ventrally by the vagina. The common opening is very close in front of the ventral sucker and within the anterior border of the genital pit. The distal bulb-like region of the male system is evidently what Linton referred to as "the prostatic portion of the cirrus pouch." Its inner wall is lined by what seems to be a layer of tall delicate cells, but these were indistinct and no nuclei could be made out. From material at hand, which seemed to be in good condition, it could not be definitely concluded that this region was glandular. As Linton studied fresh material, and as the cells in this region show very prominently in his figure (Linton 1911), his conclusion is probably correct.

The ovary is a much lobed organ located near the ventral surface a short distance posterior to the ventral sucker or about at the level of the posterior end of the seminal vesicle. The vitellaria are composed of numerous small follicles located nearer the dorsal surface and extending laterally across the body in the region between the ventral sucker and the anterior testes.

Linton's description is somewhat incomplete in regard to the region of the oviduct. Laurer's canal is present. It follows a practically straight course from the dorsal surface to the oviduct. Just before it enters the oviduct, it enters the very large, spherical seminal receptacle. This conspicuous organ is located just dorsal to the ovary and between it and the posterior end of the seminal vesicle (Fig. 83). The common vitelline duct is long, and enters the oviduct shortly beyond the entrance of Laurer's canal. The relations of these ducts are shown diagrammatically in Figure 81. A few small cells about the oviduct in this region probably represent a poorly developed ootype. The uterus coils posteriorly on the left side of the body, returning on the right. When it has returned to about the level of the ovary, it extends across the body and proceeds anteriorly on the left side of the seminal vesicle to join the ejaculatory duct. There is a very short genital sinus. The eggs measure 22 by 10 to 12 $\mu$ .

The large pyriform cells in the cortical parenchyma region of the anterior part of the body were noted. Linton suggests that they represent

yolk-forming cells, but present material offered no evidence as to their function.

*DEROPRISTIS INFLATA*\* (MOLIN 1859)

From intestine, *Anguilla chrysypa*, Woods Hole.

This well-known parasite of the eel has already been clearly and fully described by Odhner (1902). The only other species in the genus is *D. hispida* (Rud.) from the sturgeon. Stafford (1904) records *D. inflata* from the eel, but Linton does not report it from Woods Hole.

The lateral expansions of the neck region are very characteristic for the genus. The body is covered with spines which are larger on the neck expansions and on a hump-like region on the dorsal surface opposite the pharynx. Odhner sees in the spined neck-expansions the fore-runner of the spined collar of *Echinostoma*. The two suckers are small and about equal in size. The testes are located in the extreme posterior end of the body, the ovary being about in the mid-body region. The vitellaria of small follicles extend in lateral and dorsal body regions from a point about half way between the ovary and ventral sucker to the anterior end of the anterior testis. The genital pore is median close in front of the ventral sucker. The genital sinus is tube-like. Both cirrus and vagina are prominent and armed with spines as in *Stephanochasmus*, a related genus.

The number of neck spines could not be counted, but the species can be assigned to *D. inflata* on (1) body size, (2) relatively short genital sinus, and (3) egg size. The body size varied from about 0.8 mm. to 4. mm. The genital sinus has a length about equal to the diameter of the ventral sucker. The egg size was 43 to 48 by 20 to 22 $\mu$ .

*ACANTHOCOTYLE VERRILLI* GOTO 1899

[Figs. 86-88]

From Body surface, *Raia erinacea* (Bonnet skate)

A single specimen of a trematode which seems to belong to this species was obtained from *Raia erinacea*. The parasite was found in the content of the spiral valve but this was, of course, an accident. It is an ectoparasitic form. The species was described by Goto in 1899 from a single specimen sent him by Verrill who obtained it from the surface of a "skate" (from Cape Cod).

In regard to general shape and form, Goto (1899:284) says: "... the body is of almost uniform breadth, and presents a slightly concave border anteriorly. There is also a distinct constriction at the level of the pharynx. The posterior sucker is large and circular, and has 34 radii consisting of

\* Collection of Dr. H. B. Ward, vials no. 22.217 and 22.218.

\* Collection of Dr. H. B. Ward, vial no. 13.72.

numerous hollow chitinous hooks. These radii leave the central area of the sucker free, and the most posterior four or five pairs gradually decrease in length backwards, so that there is a backward extension of the central area. The longest radii consist of about eleven hooks and the shortest of only four." This description of body shape, and posterior sucker fits the present specimen exactly, except that the posterior sucker of the latter has 32 radii of hooks. But Goto's figure shows 32 instead of the 34 described in the text, so that this latter number is probably a misprint. In regard to the small accessory sucker, Goto says: "At the hind end of the posterior sucker there is, in the median line, a roundish appendage armed with filiform chitinous hooks somewhat like the upper part of an interrogation point. I cannot exactly state the number of these hooks, but I counted more than twenty." These hooks were very clear in my specimen. There were 14 hooks arranged about the circumference of the sucker and two larger hooks in the center (Fig. 87). The body size of my specimen was 3.3 mm. by 0.93 mm. The diameter of the posterior sucker was 1.33 mm. and that of the accessory sucker 0.1 mm.

Goto claims that the anterior suckers are absent in this species and that "their places are occupied by two invaginations of the investing membrane of the body. . . . The invaginations are narrow and deep, and appear like slits in the mounted specimen" (p. 284). He claims a similar condition for *A. lobianchoi* and believes Monticelli mistaken in referring to the invaginations as suckers. Monticelli (1904:73-74) disagrees with this view, pointing out that suckers are actually present but often quite completely retracted. Monticelli, in studying many individuals of this genus, found most varying appearances of the suckers due to contraction. The complete embedding of the suckers in the body by contraction is a very common reaction to the killing solution. Monticelli interprets Goto's figure as showing this condition. Study of my specimen supports Monticelli in this view. The elongate suckers with lip-like borders were clearly separate, especially at their margins, from the body wall although the internal boundaries of the suckers were indistinct.

The mouth is median and ventral about 0.26 mm. from the anterior end. It leads directly into a large, somewhat triangular-shaped pharynx. No esophagus could be seen. The intestine branches immediately and the ceca extend to the posterior end of the body.

There are about 52 testes. The exact number was difficult to determine as some of these organs were so close together as to seem double in nature. Goto gives the number as only 37. The number is probably variable. They fill the inter-cecal space of the body in the posterior two thirds of its length. The seminal vesicle shows the regions characteristic of the genus.

The ovary is spherical. It is located about  $\frac{1}{3}$  from the anterior end and slightly to the left. The two vitelline ducts lead to a point at its

anterior end. The vitellaria are extensive and well developed. They consist of large compact follicles, flattened against each other longitudinally. They are located laterally on each side of the body, and partially surround and conceal the intestinal ceca.

Monticelli (1904) questions Goto's observations on the sexual openings. Goto himself says (1899:285): "The terminal portions of the genital ducts could not be satisfactorily made out in the single specimen at my command." Goto figures a single, common genital pore on the right side of the body in the neck region. There are, however, normally in this genus three sexual openings, one lateral opening of the metraterm, while the male aperture is close to the opening of the vagina in a more median position (cf. Monticelli 1899, Tav. 1, fig. 6; Tav. 2, figs. 29-31). Monticelli (1904: 71-72) concludes from Goto's figure and description that actually . . . . "the mouths of the genital ducts are arranged, fundamentally, as in all the other species of the genus." My material shows Monticelli to be correct. The male aperture is very close to the opening of the vagina at about the level of the forking of the intestine and slightly to the right. What Goto interpreted as the common genital pore is actually the opening of the metraterm. It is located laterally on the right side of the body. From it protrudes in my specimen a cluster of three eggs. These eggs are bright yellow in color and measure 0.428 by 0.085 mm. The stalk-like basal region of the eggs was inserted in a swollen terminal region of the metraterm.

Monticelli (1904) also expresses the conviction that Goto was wrong in regard to the metraterm opening to the right of the ventral face, believing that further study would show it to be on the left as in other species of *Acanthocotyle*. He suggests that Goto might have confused the dorsal with the ventral surface. In my specimen there is no doubt, however, that the pore is on the right side. The mouth opening could be made out so that the ventral surface was definitely ascertained. There remains the possibility that both my specimen and that of Goto represent cases of amphitypy, as, indeed, Monticelli suggests might occur in this group as found by Cerfontaine (1900:449) so common among the *Octocotylides*. Only more abundant material can settle this point.

### *DACTYLOCOTYLE MINOR* (OLSSON 1868)

[Figs. 84-85]

Synonyms: *Octobothrium palmatum* S. *minor* Olss. 1868.

*Octobothrium minus* Olss. 1876.

From Gills, *Urophycis chuss* (Squirrel hake)

This species was first named by Olsson (1868:18) as a variety of *O. palmatum* Leuckart. In 1876, Olsson (1876:10) named it *Octobothrium minus* n. sp. Cerfontaine (1898:302) observed that this species was prob-

ably a true *Dactylocotyle* species. Saint-Remy (1898:55) listed it as "*Dactylocotyle minor* Olss." Stiles and Hassall (1908) list the species as "*Dactylocotyle minor* Saint-Remy." As Olsson's original description of *O. palmatum* f. *minor* is fairly complete and accompanied by a figure, and since sub-specific names follow the same rules as specific names, there can be no reason for not retaining Olsson's original name *minor*, as Saint-Remy, in fact, did. The correct name is then *Dactylocotyle minor* (Olss.) Saint-Remy.

The following is a diagnosis of this species as given by Saint-Remy (1892:41): "Body flattened, divided into two parts by a deep indentation; anterior part lanceolate-oval, the posterior or caudal part much shorter than the anterior, provided with canals, carrying on each side 4 marginal pediceled suckers, pedicels cylindrical, equal. Testes in the median anterior part. Length 3 to 6 mm., width 1.5 mm. On gills of *Gadus melanostomus*."

Three specimens were collected from the gills of a single fish. Examination of numerous other fish showed no infection, so the parasite is probably not a very common one. In some respects the form seems to differ slightly from *Dact. minor*, but in view of the fact that body contraction partly explains these differences and that only three specimens were collected, they are referred to this species.

Stafford records *Dactylocotyle phycidis* from the gills of the squirrel hake in Canada. Considering the identity of region and host, it is probable that he was dealing with the form now being considered. The species cannot be referred to *Dact. phycidis* (although the hosts are similar) because of its marked difference in size, shape, and number of hooks in the genital sucker. It is like *Dact. palmatum* in possessing a common genital opening, 14–16 hooks in the genital sucker, and in having few non-filamented eggs in the vagina. Olsson's variety *Dact. palmatum minor* differs from *Dact. palmatum* in its smaller size and in the sharp division of its body into two regions.

In my material, the posterior region bearing the pediceled suckers or pincers was so distinctly cut off from the body proper as to appear appendicular (Fig. 84). Except for small branches from the intestine which invade this posterior part, all the organs are located in the anterior region.

The anterior region is flattened and broadly oval in shape. In life it is of a gray color. The surface of the body is not entirely smooth, and in this respect my material differs from the descriptions of all other representatives of the genus. Minute scale-like plates give the body a roughened surface particularly in posterior body regions and on the pedicels of the suckers. These scales are less conspicuous anteriorly where the body seems quite smooth.

Other features are in accord with descriptions of the genus. The posterior suckers are provided with a very complicated system of chitinous



supporting rods which make the suckers more like pincers in function. On each side of the mouth which is at the anterior tip of the body there is a small lateral sucker. A globular pharynx is present. The ceca of the intestine are profusely branched and the fine branches ramify throughout the whole body.

The genital pore is located on the ventral surface about 0.3 mm. from the anterior end. Its position can be located by the conspicuous genital bulb or sucker. This sucker actually surrounds the distal portion of the male duct. It is provided with a ring of 14 hooks (Fig. 85). The number of hooks in the genital sucker varies within narrow limits in a species. The testes are numerous. Packed closely together, they fill most of the mid-body region of the anterior part of the worm. The seminal vesicle is located far forward, dorsal and slightly posterior to the genital sucker. It is much coiled. Between it and the genital sucker is a swollen, bulb-like region with very thick walls. This structure is about the size of the pharynx near which it is located.

The compact and dense follicles of the vitellaria fill the sides of the body and almost meet just anterior to the ovary. The ovary is slightly but tightly coiled so that it is compact S-shaped. There is a large coiled seminal receptacle located slightly anterior to the ovary. An ootype and small yolk reservoir lie ventral to the ovary. The uterus leads a straight course anteriorly and joins the male duct ventrally outside the genital sucker and close to the genital pore. Only one non-filamented egg was found in the uterus.

Measurements on two specimens are as follows:

Length.....	2.8 mm.	2.9 mm.
Width.....	1.6 mm.	1.75 mm.
Oral sucker.....	0.108	0.114
Genital sucker.....	0.074	0.085
Egg.....	0.159 by 0.017	
Longest diameter of posterior suckers—1..	0.188	0.199
2..	0.245	0.21
3..	0.381	0.228
4..		0.399

## SUMMARY AND CONCLUSIONS

A general collection of entozoa of marine fish was made at Mt. Desert Island, Maine. Of these parasites, the trematodes were selected for study.

Particular attention was given to *Otodistomum cestoides* from the stomach of *Raia stabuliforis*. The morphology of this form was studied in considerable detail and compared with *O. veliporum*, material of which from *Raia binoculata* was available. The two species were found to be even more similar than hitherto recorded, but were distinct in a marked difference in egg size. The extent of the vitellaria varied considerably and this feature cannot be used to separate species in this genus. The internal longitudinal parenchyma muscles were found to be somewhat scattered in these forms, but definitely external to the vitellaria, a condition to be contrasted with their position in the related genus, *Azygia*. The prominent genital papilla hitherto considered as a permanent structure in *Otodistomum* was found to have the capacity (in both species) of being completely flattened out, or completely protruded. It was found to be usually much less prominent in *O. veliporum*.

The growth changes of *O. cestoides* within its final host were studied from measurements on over 200 specimens. Conspicuous changes in size are associated with regional changes in body proportions. Growth results chiefly in body elongation and occurs chiefly posterior to the ventral sucker. The region of the uterus slightly increases its size ratio to other body parts after sexual maturity, but the tail region alone also maintains a constant proportional growth increase as compared with the region anterior to the ventral sucker. The two suckers maintain a constant proportional size in respect to each other. Both suckers are relatively much larger in young forms.

Live miracidia of *O. cestoides* were readily obtained by the hatching of eggs secured from adult worms. These eggs at the time of deposit contain mature larvae ready to hatch. The egg shell is, however, very thick. It was discovered that the hatching of the eggs was stimulated by evaporation of the sea-water in which they were kept. Eggs in cultures submerged in aquaria did not hatch. Larvae were obtained as early as five hours after removal of eggs from the worm. All indications point to the conclusion that the eggs do not normally hatch until eaten by the intermediate host.

The miracidium of *O. cestoides* was found to be unciliated. Its form and shape vary with the worm-like extension and contraction of the body. The anterior end of the larva is continually being retracted and extended

like a proboscis. The miracidium has no apparent capacity for locomotion. A conspicuous internal organ of the miracidium has been commonly interpreted as an intestine. It was found that this organ was four-partite in structure. Each part evidently consisted of one cell with a large nucleus. The organ therefore cannot be regarded as an intestine, but probably represents a group of unicellular glands.

The eggs of *O. cestoides* are eaten by snails kept in the same vial with them. This eating of the eggs was conspicuous only in the case of the common gasteropod, *Littorina littorea*. Larvae were found hatching in the intestine of this snail in two cases.

The entire family Azygiidae was studied in an attempt to clear up an evident confusion in that group especially in American forms. The type material of most American species of *Azygia* and related genera was studied. It was found that all American representatives (consisting of eleven recorded forms) could all be referred to three species of *Azygia* as follows: *Mimodistomum angusticaudum* Staff. and *Azygia loossii* Marshall and Gilbert to *Azygia angusticauda* (Staff.); *Dist. longum* Leidy, *Dist. tereticolle* of Leidy, *Megadistomum longum* (Leidy), *Azygia tereticolle* of Stafford, *Azygia sebago* Ward, *Azygia bulbosa* Goldberger, *Hassallius hassalli* Goldberger, and *Azygia lucii* of Cooper to *Azygia longa* (Leidy). *Azygia acuminata* Goldberger was retained. Apparent differences between many of the forms were found to be in accord with growth changes which would be expected in the group. *Azygia perryi* was also studied and found to be probably identical with the European species, *Azygia lucii*.

A general study was made of the entire trematode collection from Mount Desert Island. A few forms from Woods Hole are also considered. Twenty different species belonging to eighteen different genera are identified. A number of these are described at some length.

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## EXPLANATION OF PLATES

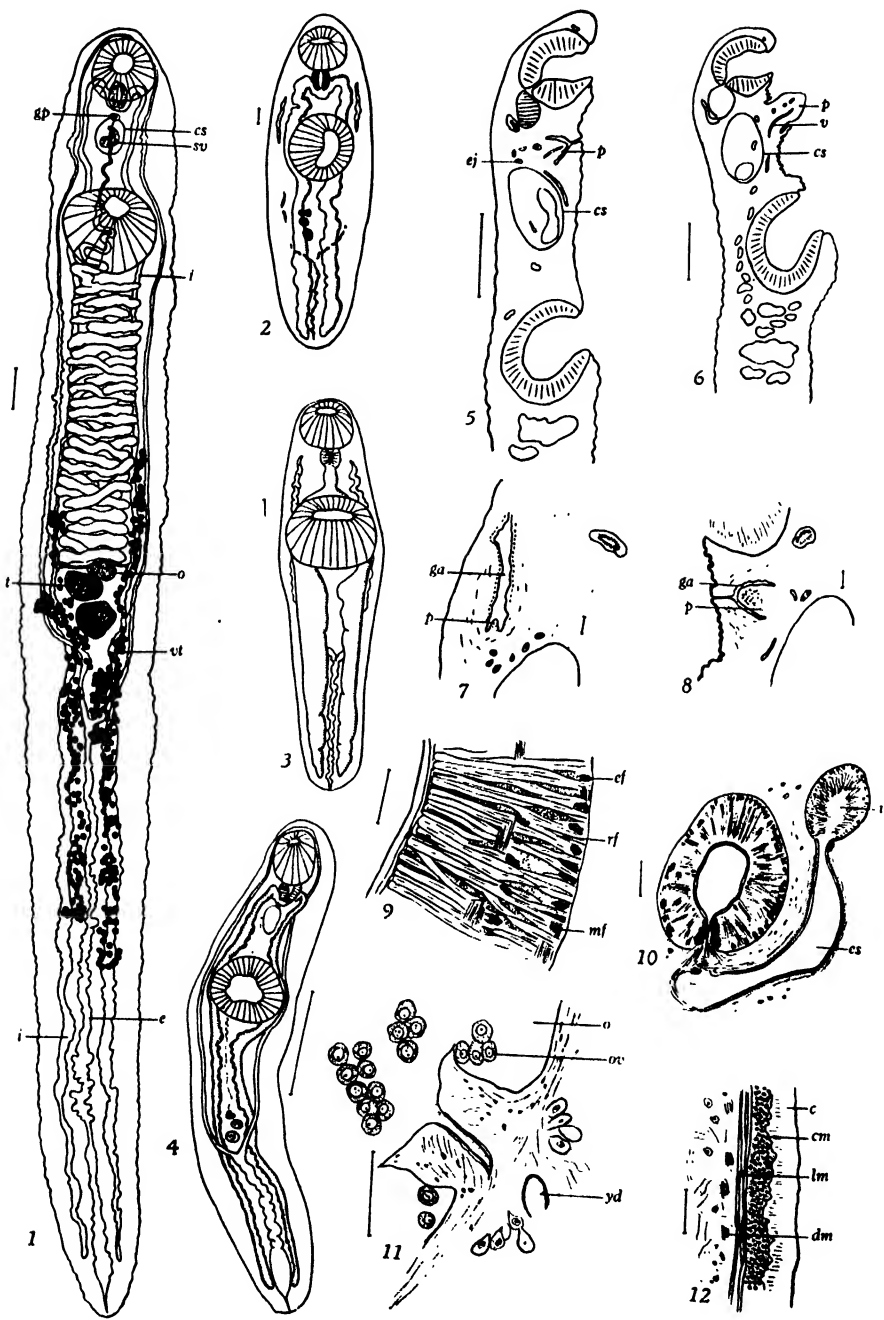
With the exception of Figs. 3, 76, 77, and 81, all figures were drawn with the aid of a camera lucida. The scale projected is equal to 0.1 mm. unless otherwise indicated in the explanation of figures. The following abbreviations are used:

<i>a</i>	tail appendage	<i>lm</i>	longitudinal muscles
<i>ac</i>	accessory sucker	<i>mf</i>	meridional fibers
<i>as</i>	anterior sucker	<i>mo</i>	male sex opening
<i>c</i>	cuticula	<i>o</i>	ovary
<i>cd</i>	common sex duct	<i>od</i>	oviduct
<i>cm</i>	circular muscles	<i>ot</i>	ootype
<i>cs</i>	cirrus sac	<i>ov</i>	ovum
<i>dm</i>	diagonal muscles	<i>p</i>	genital papilla
<i>dp</i>	duct of prostate gland	<i>ph</i>	pharynx
<i>e</i>	excretory system	<i>pp</i>	prepharynx
<i>ef</i>	equatorial fibers	<i>pr</i>	prostate gland
<i>ej</i>	ejaculatory duct	<i>rf</i>	radial fibers
<i>es</i>	esophagus	<i>s</i>	spermatozoa
<i>f</i>	genital fold	<i>sr</i>	seminal receptacle
<i>fo</i>	female sex opening	<i>sv</i>	seminal vesicle
<i>ga</i>	genital atrium	<i>t</i>	testis
<i>gc</i>	gland cell	<i>u</i>	uterus
<i>gp</i>	genital pore	<i>v</i>	vagina
<i>gs</i>	genital sinus	<i>vs</i>	ventral sucker
<i>i</i>	intestine	<i>vt</i>	vitellaria
<i>lc</i>	Laurer's canal	<i>yd</i>	yolk duct

## PLATE I

## EXPLANATION OF PLATE I

- Fig. 1. *Otodistomum cestoides*. Ventral view of adult. Scale=1 mm.  
Fig. 2. *O. cestoides*. Ventral view of young specimen.  
Fig. 3. Copy of Nicoll's figure of cercaria of *O. cestoides* from cyst from flounder. Enlarged to same proportion as Figure 2.  
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Fig. 6. Same, with genital papilla protruded. Scale=1 mm.  
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Fig. 11. Cross-section through edge of ovary of *O. veliporum* showing beginning of oviduct.  
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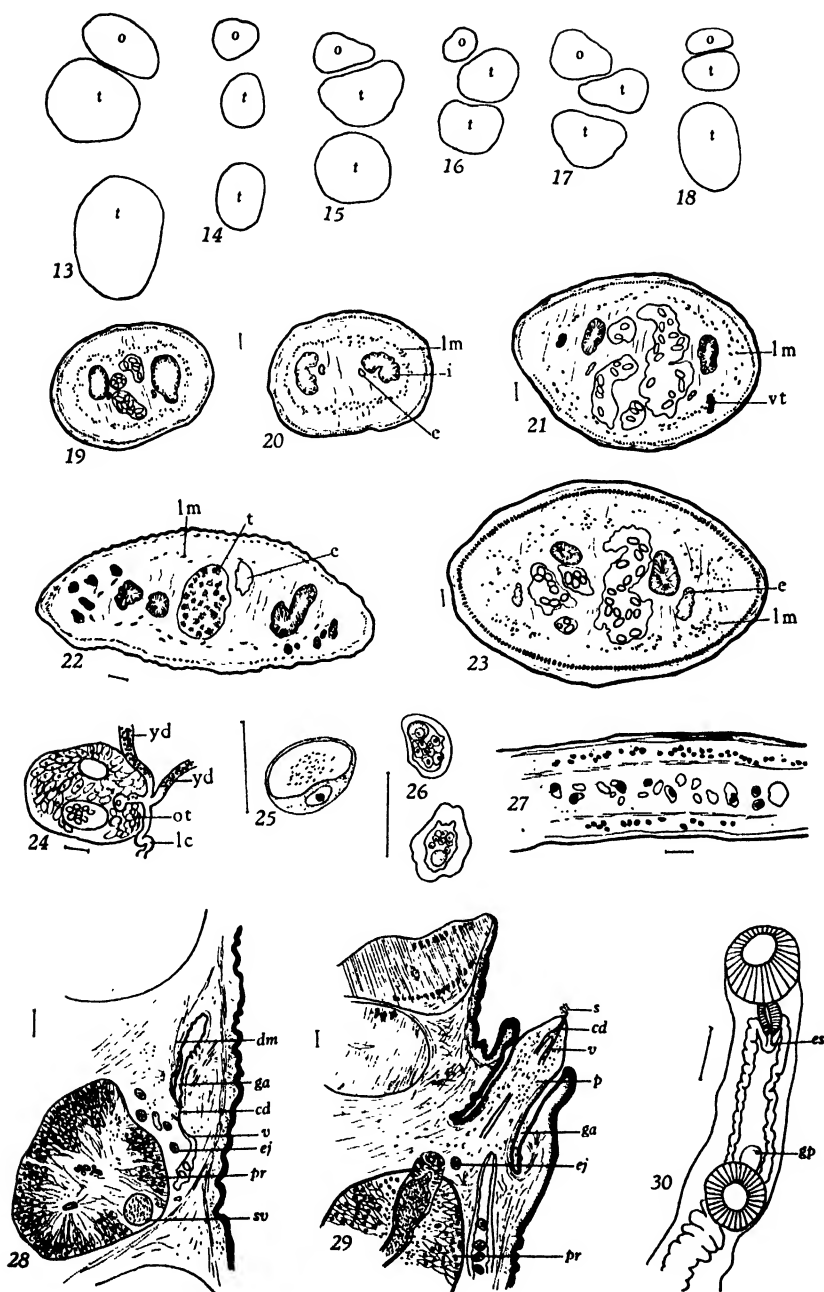




## PLATE II

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- Figs. 13-18. Outline drawings of gonads in *O. cestoides* to show changes in relative position of ovary.
- Figs. 19-20. Cross-sections of *Azygia sebago* to show inner parenchyma muscles.
- Figs. 21-22. Same of *A. acuminata*.
- Fig. 23. Same of *Otodistomum cestoides*.
- Fig. 24. Ootype region of *O. cestoides* to show relations of ducts. Semi-diagrammatic.
- Fig. 25. Cross-section through vas deferens of *O. cestoides*. Scale=0.05 mm.
- Fig. 26. Sections through early eggs of *O. cestoides* before shell has assumed regular form.
- Fig. 27. Frontal section through uterus region of *Azygia angusticauda*, showing inner parenchyma muscles.
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- Fig. 29. Same of *O. veliporum* showing genital papilla protruded.
- Fig. 30. Ventral view of anterior body region of *Azygia longa* showing position of genital pore. Scale=1 mm.



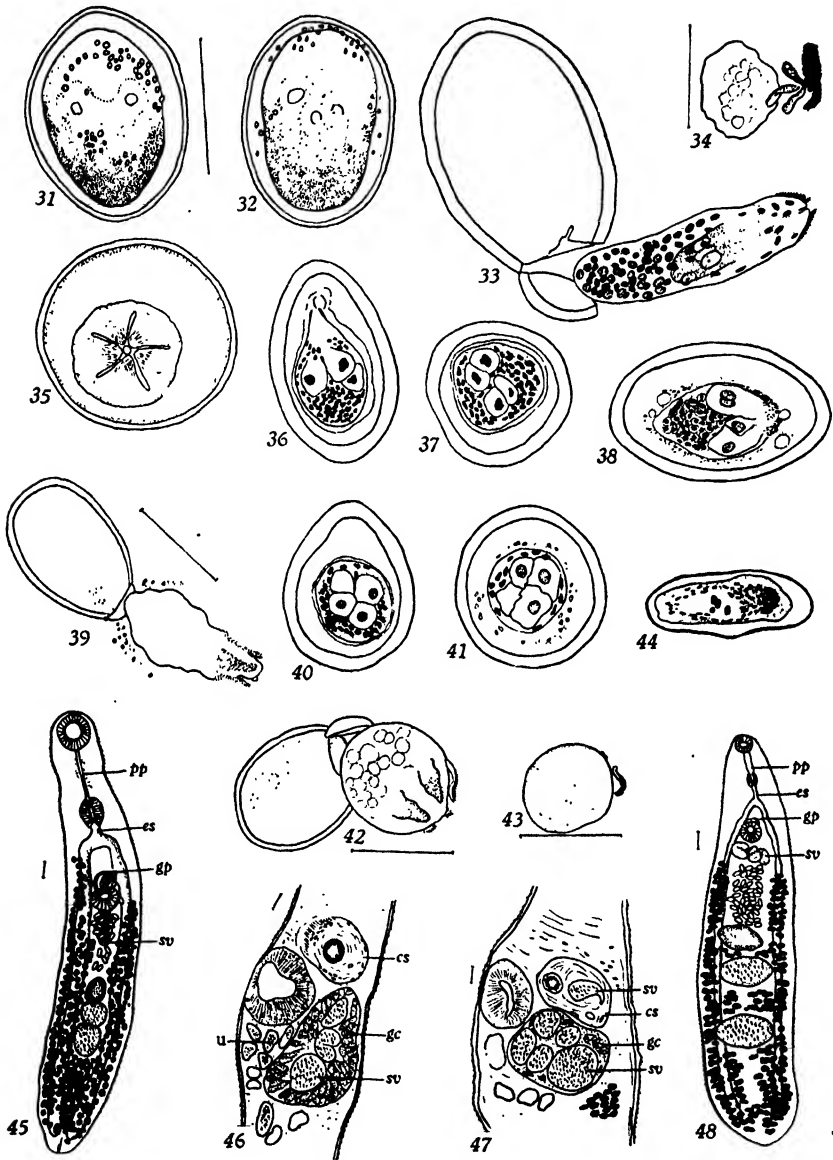




## PLATE III

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- Fig. 31. Mature egg of *Otodistomum cestoides*. Drawn from live egg. Scale=0.05 mm.
- Fig. 32. Same, showing three lobes in internal organ. Scale=0.05 mm.
- Fig. 33. Miracidium and empty egg shell of *O. cestoides*. Drawn from toto-mount. Length of larva 91 $\mu$ .
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- Fig. 36. Longitudinal section through mature egg of *O. cestoides*, showing paired glands.
- Fig. 37. Cross-section of same.
- Fig. 38. Longitudinal section through mature egg of *O. veliporum*.
- Fig. 39. Recently hatched miracidium of *O. cestoides*. Drawn from live specimen. Scale=0.05 mm.
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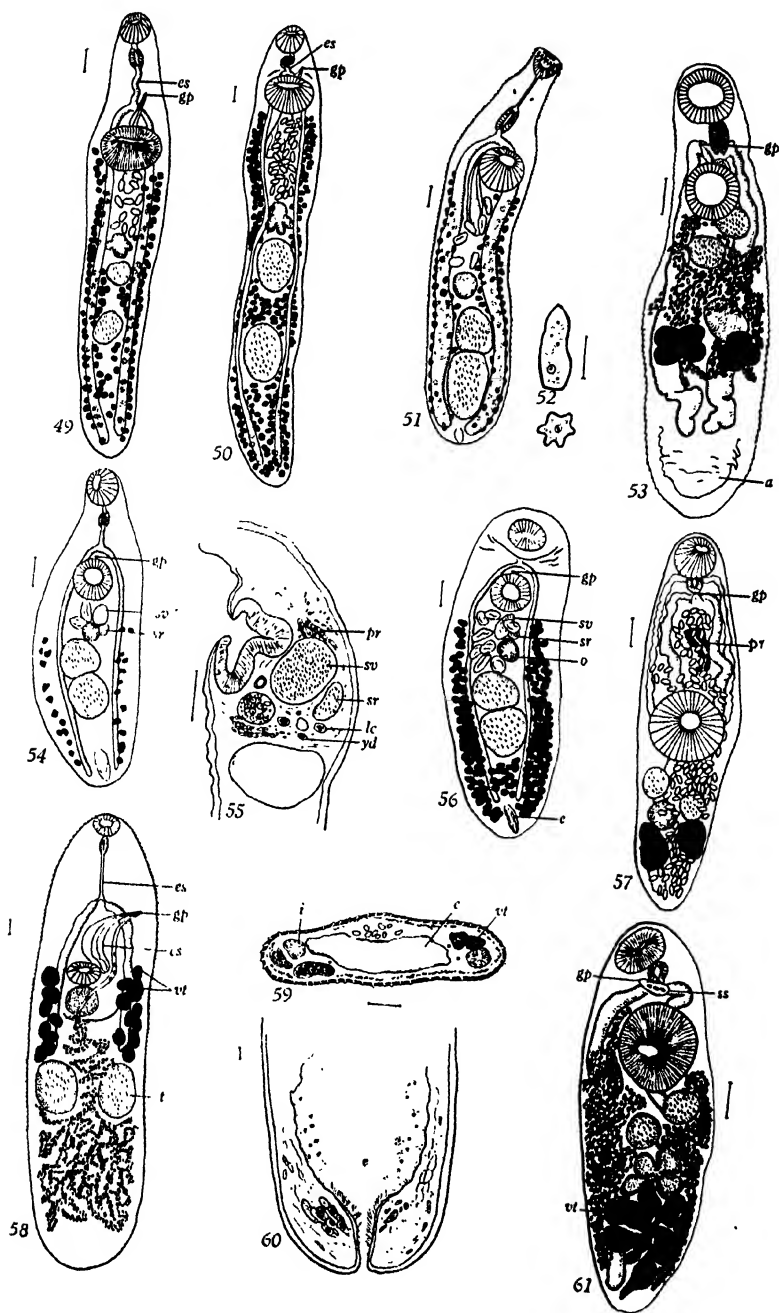




**PLATE IV**

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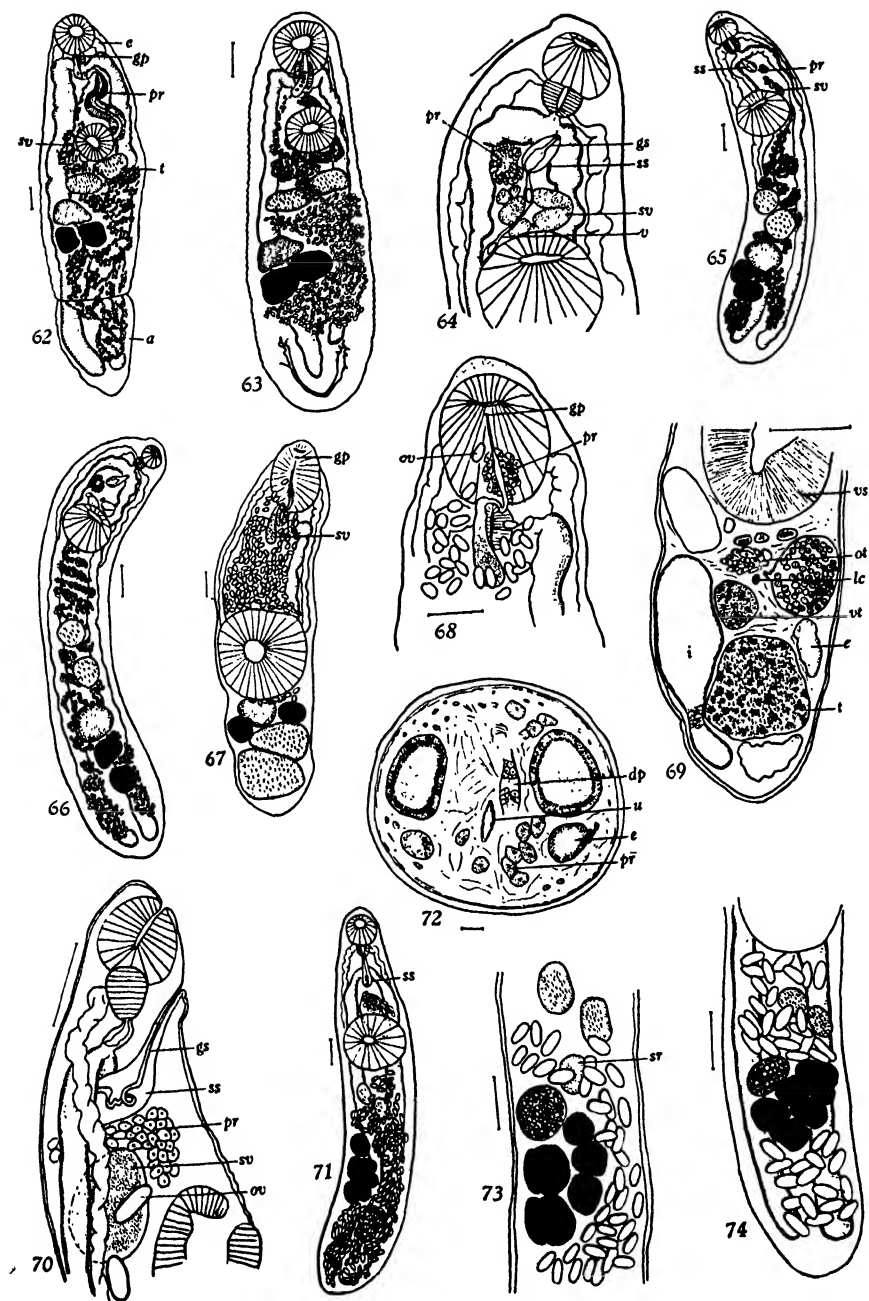




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# COMPARATIVE STUDIES ON FURCOCERCOUS CERCARIAE

WITH 8 PLATES AND 2 TEXTFIGURES

BY  
HARRY MILTON MILLER, JR.



# **THESIS**

**SUBMITTED AS PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE  
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## INTRODUCTION

Early in the study of larval trematodes, begun in 1920 at the suggestion of Professor Henry B. Ward, the author's interest became centered on the furcocercous cercariae, and exclusive attention was devoted to these forms. In this work all larvae which possess a tail with a bifurcated distal end have been considered, although the heterogeneity of the group is recognized and was, indeed, a reason for the present study; these forms are also of interest because of the relation of some of them to schistosomiasis.

Collections of the common pulmonate snails, *Planorbis* and *Physa*, from the Drainage Ditch, Urbana, Illinois, as well as from small streams running into it, yielded furcocercous cercariae. Species of branchiate snails of the genera *Goniobasis* and *Campeloma* from several localities were also examined, but no furcocercous infections were found. During the summer of 1921 the investigations were carried on at the University of Michigan Biological Station at Douglas Lake, Michigan; various species of pulmonate and branchiate snails were collected from the waters of this region. Complete collection and infection records are given in another part of this paper.

As a result of this study seven new species of furcocercous cercariae are added to the fauna of North America; and the author is able, from a personal knowledge of some partly described forms, and with the advantage of access to recent literature, to present a survey of this group of larval trematodes.

To Professor Henry B. Ward, under whose direction the investigations have been carried out, the author acknowledges indebtedness for suggestions and helpful criticisms, and for the use of his extensive private library. Thanks are also due to Dr. G. R. LaRue, Director of the Michigan Biological Station, for courtesies extended during the summer of 1921, and to Professor Frank Smith and Curator Frank C. Baker of the University of Illinois for the identification of snail hosts.

## HISTORICAL REVIEW

Probably the first furcocercous cercaria to be described is included by O. F. Müller (1773) in the *Vermium Terrestrium et Fluviatilium*; he placed it in the genus *Vibrio*, as *Vibrio malleus*. There is no figure, and the description is short, containing the following significant words: "motu literam Y, quiete T simulat." This form was accepted by subsequent workers as a cercaria. In 1794 Abildgaard described a larval trematode from Denmark with a tail distally bifurcated to its middle, to which he gave the name *Cercaria varicans*. This is the first record of a larva, recognized as a trematode, having this sort of tail. The original description is very scanty, and as no details of structure were added by the few subsequent workers who discussed this form, it could not now be identified with certainty. No internal structures are either described or figured, which leaves in doubt the presence or absence of a pharynx; no ventral sucker is shown. In the figures the furcae are about equal in length to the tail-stem.

Nitzsch (1817) very briefly described *C. furcata*, a distome larva with relatively long furcae sharply delimited from the tail-stem; this form has been mentioned by a number of authors but no significant details have been added. Diesing (1850), in his *Systema Helminthum*, included *Malleolus furcatus* Ehrenberg (1838) as the only known species of distome furcocercous larva, and listed the following as synonyms: *Vibrio malleus* Müller (1773), Zirkelthier of Eichhorn (1781), *Histrionella fissa* Bory (1825), *Cercaria furcata* Nitzsch (1817), and *Cercaria* VI von Baer (1826). This synonymy, with the exception of *Histrionella fissa*, was accepted by Moulinié (1856), who did not recognize the genus *Malleolus*, but listed the synonyms under *Cercaria furcata* Nitzsch. The present author finds no evidence in the literature which would set aside the disposition of Moulinié; in every case the accounts are so meager, with an almost complete lack of description of internal structure, that the species could not be identified with certainty. Diesing, in the *Systema Helminthum*, placed *Cercaria varicans* Abildgaard in a new genus *Cheilostomum*, as *Cheilostomum varicans*, the type and sole species; Moulinié returned this species also to the genus *Cercaria*.

La Valette St. George (1855) included in his monograph on larval trematodes brief descriptions of four new furcocercous forms, a brevifurcate monostome, *Cercaria cristata*, and three distomes, *C. fissicauda*, *C. gracilis*, and *C. ocellata*. He also figured *C. dichotoma* Joh. Müller, said to have been found by Müller in 1850 in the Mediterranean at Nice. This paper by Müller does not contain any definite reference to a furcocercous larva, and

the figure included by La Valette St. George has been accepted by subsequent workers. *C. dichotoma* is the first of the few marine furcocercous cercariae which have been described. Filippi (1857) questioned the validity of *C. cristata*, as being distinct from *C. varicans*. The present author is of the opinion that they are distinct, because the dorsal body crest, prominent in *C. cristata*, was not mentioned or figured by Abildgaard for *C. varicans*; furthermore the latter species is a longifurcate larva, while the former is brevifurcate.

Diesing (1858), in a further systematic treatise on cercariae, made a new genus *Lophocercaria* to contain only *Lophocercaria fissicauda*, under which he put as a synonym *Cercaria cristata* La Val. St. George; there is no reason, stated or apparent, for such a change of specific name. Two other species of La Valette St. George were placed in a new subgenus, *Cercaria* (*Schizocerca*) *gracilis* and *C. (Schizocerca) fissicauda*, as well as *C. (Schizocerca) dichotoma* Joh. Müller. He also established the genus *Histrionellina* to contain only *Cercaria ocellata* La Val. St. George, which was designated *Histrionellina fissicauda*. No significant details of structure were added to previously described forms by the investigations of Pagenstecher (1857), Wagener (1866), or Villot (1875). Ercolani (1882) briefly described three new species, a brevifurcate monostome, *Cercaria microcristata*, and two longifurcate distomes, *C. aculeata* and *C. minuta*. Morgan (1891) reported the finding of one individual, which he decided was a new species of marine larval trematode, taken in a tow at Jamaica; while his single sketch shows a bifurcated tail, very small in proportion to the body, it is not known whether this cercaria is too aberrant to be included with other furcocercous forms.

Sonsino (1892) briefly described the first fresh water furcocercous larva to be reported outside of Europe, *Cercaria vivax* sp. inq. from Egypt. In a short note (1894) he indicated that there were three pairs of flame cells in the tail-stem of this cercaria; this is the first record of the tail flame cells, which are unique for the furcocercous larvae. The work of Looss (1896) made this the first furcocercous larva to be described with respect to the excretory system pattern in the sporocyst and its development in the cercaria. By his studies was established the bilateral embryonic character of the caudal excretory tube, which is unpaired in the mature cercaria; he figured the presence of an island in the excretory tube at the juncture of body and tail-stem. The branches of the caudal excretory tube which pass through the bifid portions of the tail were described as opening near the tips. A subterminal birth-pore was described and figured at the anterior end of the sporocyst. The differences between the much modified oral sucker of *C. vivax* and the typical sucker of larvae without forked tails were clearly recognized by Looss, who also noted and described about eight gland cells within this modified sucker. Thus *C. vivax* is the first furcocer-

cous cercaria for which there is a careful and complete description. Sonsino (1897) briefly reported a furcocercous distome, *C. bipartita*, from Italy; in contrast to all previously described forms, it was said to develop in rediae.

Haswell (1902) described a marine larva, which, although it apparently belongs to the echinostomes, has a distally bifurcated tail and an excretory system in the body more like the furcocercous than the echinostome cercariae; no flame cells or tubules were seen in the tail. Pelseneer (1906) described *C. syndosmyae* from *Syndosma alba*, a marine mollusc. Lebour (1908) studied *C. dichotoma* Müller, and figured both sporocyst and cercaria.

In his treatment of the trematodes of the fresh waters of Germany and surrounding countries Lühe (1909) briefly summarized the descriptions of the furcocercous larvae; of the ten fresh water species of Europe one, *C. varicans* Abildgaard, was not included. In the scheme of classification the monostome furcocercous larvae, which are characterized by a median dorsal crest, were grouped as the Lophocercariae, and the distomes as the Furcocercous Cercariae. In the key these last were subdivided on the basis of presence or absence of eye-spots, the degree to which the furcae were delimited from the tail-stem and whether development took place in rediae or in sporocysts. Brief notations of two incompletely described forms, which were not named, were also included. The brevity of the descriptions in Lühe's work shows how incompletely these early species are known, a condition in contrast with the work of Looss on *C. vivax*.

Ssinitzin (1909) studied *C. ocellata* and described its morphology and behavior in detail. Two differentiated sets of large unicellular gland cells, occupying the greater part of the body, were reported for the first time in a furcocercous larva, an anterior group from which the contents had been largely dissolved out and a posterior group containing coarse granules. These glands, later designated salivary glands by Ssinitzin (1911), and cephalic, poison, mucus, mucin, salivary-mucin by other authors, are in the present paper termed penetration glands. Although seven pairs of flame cells were noted as being present in the body of *C. ocellata*, they were unfortunately omitted from the two drawings referred to, and the pattern of the excretory system is therefore unknown. The presence of a greatly modified organ in place of an oral sucker, divided into an anterior thin-walled and a posterior muscular portion as subsequently described for schistosome larvae was noted; within, gland cells were seen, later designated as the head gland by Narabayashi. The type of alimentary canal which opens on the antero-ventral surface by a capillary tube was also figured. Blochmann (1910), in a paper which seems to have escaped general notice, called attention to the fact that death resulted to several species of fish and to axolotyl and salamander larvae from the penetration of great numbers of *C. fissicauda*. Their further development was not studied. The results of compre-

hensive studies on the stages of digenetic trematodes infesting molluscs of the Black Sea were published (in Russian) by Ssnitzin (1911); one furcocercous larva, *C. discursata*, was described. He proposed the term parthenita for the mature sporocyst or redia; and salivary glands for the very large gland cells (penetration glands) frequently occupying the greater part of the body, as in *C. ocellata*, and discharging through heavy ducts opening at the anterior tip of the body.

Odhner (1911) published a brief account of some investigations which Looss had made on the life history of *C. cristata*, and included two sketches of that larva; the excretory tube in the tail-stem bifurcates and passes through each furca, but it is not shown where these branches open to the exterior. A marine cercaria was briefly described by Odhner (1911a) and believed to be the larva of *Haplocladus minor*; no figures of the cercaria were published. Lebour (1912), in a review of British marine cercariae, objected to Lühe's (1909) use of tail form in the classification of larval trematodes, and proposed to divide all cercariae into two primary groups, on the basis of development in sporocyst or in redia. Division of the British marine larval forms was made on this basis; *C. dichotoma* was the only furcocercous form considered.

In 1912 da Silva reported a brevifurcate distome larva, *C. blanchardi*, from Brazil; this is the first record of a furcocercous cercaria from South America. In the brief description and microphotograph it resembles the human schistosome larvae, and is considered by Lutz and others to be probably the cercaria of *Schistosoma mansoni*. Miyairi and Suzuki (1913; in Japanese) determined the infective stage of *Schistosoma japonicum* to be a brevifurcate distome larva. The same authors (1914) published descriptions of the parthenita and cercaria, together with two plates. The cercaria was described as possessing three pairs of large penetration gland cells, and the locations of five pairs of flame cells, four pairs in the body and the fifth in the tail-stem, were indicated. A granular mass in the modified oral sucker was described, and is undoubtedly the structure later designated as the head gland. Ogata (1914) also described the cercaria of *S. japonicum*. His report of the number of flame cells agrees with that of Miyairi and Suzuki. The three pairs of penetration glands were designated poison glands, and the alimentary canal posterior to the modified oral sucker was correctly figured but not recognized as esophagus and cecum.

Cort (1914), in a preliminary report of studies on North American larval trematodes, described one furcocercous form, *C. douthitti*; the presence of "eight large unicellular glands, which seem to be analogous to the stylet glands in certain other forms" was noted. In the complete publication (1915) he gave a more detailed structural analysis of *C. douthitti*, in which the term cephalic glands was used for the penetration gland cells. Both Lühe's (1909) and Lebour's (1912) classifications of cercariae were



discussed and that of the former followed; Cort adopted the term furcocercous from Lühe for larvae with distally bifurcated tails, of which *C. douthitti* was the first North American form to be described. Concerning the group Cort stated (1915:51): "The furcocercous or forked-tailed cercariae are very imperfectly known. The anatomy of only a few of the known forms is at all well worked out and the life-history of no one of them has been determined. At least a dozen species have been reported as distinct, some of which, however, have been described very briefly in the older accounts. Sufficient evidence is not available to justify any conclusions as to the natural or artificial character of this group."

Leiper and Atkinson (1915) briefly described the primary and secondary sporocysts and the cercaria of *Schistosoma japonicum*, and also included a record of the presence of a larva (see figure 6 of Leiper and Atkinson) closely resembling *C. vivax* Sonsino. Their account of the cercaria of *S. japonicum* differs from those of Miyairi and Suzuki (1914) and Ogata (1914), in that instead of three pairs of penetration gland cells they reported five or more pairs. Leiper (1915), in the reports of the Bilharzia Mission to Egypt, presented the results of extensive investigations of the causative agents of schistosomiasis. Three distome cercariae were figured, one from *Planorbis boissyi* which upon experiment proved to be the larva of *S. mansoni*, another from *Bullinus* which was experimentally determined to be the infective stage of *S. haematobium*, and a third very large form from *Planorbis boissyi* (see figure 46 of Leiper); no attempt was made to describe these larvae in detail. All have relatively short furcae without cuticular keels, and are further similar in the lack of pharynxes and eye-spots; the figures indicate that in the equipment of the penetration glands the three forms differ. Another form, said to be very similar to *C. ocellata*, was found in three different snails; the possession of a cuticular keel along each side of the furcae, and of pigmented eye-spots anterior to the ventral sucker distinctly set it off from the schistosomes. The provisional name *C. bilharziella* was used. Two other forms were found, *C. vivax* Sonsino and *C. fissicauda* La Val. St. George; both were reported as possessing a muscular pharynx. As a result of Leiper's studies, the schistosome cercariae were differentiated from other furcocercous forms by the lack of pharynx, of pigmented eye-spots, and of cuticular keels on the furcae, which are less than one-half as long as the tail-stem. *C. bilharziella* was thought to belong to a genus closely allied to *Schistosoma*.

Cawston (1915), in the first of a long series of short papers in which South African furcocercous cercariae are meagerly described and incompletely figured, reported a new species, *C. secobii*, from *Physopsis africana*. Linton (1915) briefly described a brevifurcate monostome from *Hydroides dianthus*, and noted its resemblance to *C. cristata* La Val. St. George; it is the first marine furcocercous larva reported from North America. In a

second paper (1915a) he recorded another larva, from *Pecten irradians*, which he found to be much like that from *Hydroides*; the outline sketches do not make it possible to arrive at any conclusion as to their identity. Leiper (1916), in the fourth section of the report of the Bilharzia Mission, gave a table of Egyptian molluscs in which the various trematode larvae, including the furcocercous forms, were found. Narabayashi (1916), according to Cort's (1919) translation of Miyagawa (1916), designated the gland cells within the modified oral sucker of the cercaria of *Schistosoma japonicum* as the head gland (Kopfdüse).

Fuhrmann (1916) described a longifurcate distome, *C. letifera*, which possesses fine bristle-like hairs on the tail-stem, structures reported for the first time on a furcocercous larva. Yoshida (1917; in Japanese) described a brevifurcate distome, *Cercaria* G, which is figured as having a distinct pharyngeal bulb, a structure previously reported only for the longifurcate forms; development was said to take place in rediae. Iturbe (1917, 1917a) published a brief description, with one diagrammatic figure, of the cercaria of *Schistosoma mansoni* in South America. He reported five pairs of flame cells in the body, and three pairs of large gland cells; subsequent work on this species by other authors is not in agreement with these findings. O'Roke (1917) briefly described three new furcocercous distome larvae from Kansas, an apharyngeal form, *C. echinocauda*, and two longifurcate larvae, *C. inversa* and *C. quieta*. LaRue (1917), from a study of two agamodistomes,\* which he called *C. marcianae* and *C. vergrandis*, concluded, on the basis of staining tests with thionin and toluidin blue, that the large penetration gland cells secrete mucus (mucin). Faust (1917), in a preliminary paper, described *C. gracillima* and *C. tuberistoma*, longifurcate forms from the pulmonate gastropods of Montana. He considered the apharyngeal furcocercous cercariae to be "undoubtedly larval schistosomes as demonstrated by the experimental work of Leiper (1916) and by a close comparative study which the writer has made on larvae and adults" (p. 121).

Cort (1917), in a discussion of the homologies of the excretory system, added the exact pattern of that system to the description of *C. douthitti*, and noted for the first time areas in the walls of the bladder arms which were ciliated, organellae which in other larvae had unquestionably been mistaken for flame cells. In the excretory tube of *C. douthitti* he described the small island previously figured by Looss (1896) for *C. vivax*, and later designated by Faust (1919c) as the island of Cort. For *C. douthitti* Cort reported the number of penetration glands to be ten, instead of eight as originally found. Three new species, *C. douglasi* and *C. emarginatae*, longifurcate larvae, and one brevifurcate form, *C. elephantis*, were described,

\* One of these, more properly designated *Agamodistomum marcianae*, has been held by Cort (1918:130) to be the agamodistome stage of a furcocercous cercaria.

together with the excretory system pattern of the cercaria of *Schistosoma japonicum*. The six furcocercous cercariae discussed were divided into three groups, of which the first two were assigned to the family Schistosomatidae. Members of Groups I and II are characterized by the absence of a pharynx and by furcae definitely delimited from the tail-stem and less than half its length; members of Group I possess eye-spots which distinguish them from the larvae of Group II. The third group was created to contain the cercariae possessing distinct pharynges and with furcae which are almost as long as the tail-stem and not delimited from it. The homologies of the excretory systems in the furcocercous cercariae were discussed and the importance of this system as an indicator of relationship was emphasized.

Cawston (1917) suggested the name *C. oculata* for an apharyngeal, brevifurcate distome with eye-spots, and *C. secobiana* for a longifurcate larva. In a subsequent paper (1917a) he again briefly described *C. oculata* and *C. secobii*; later still the synonymy of *C. secobiana* 1917 with *C. secobii* 1915 was acknowledged (1917b). Faust (1918) described *C. gracillima* and *C. tuberistoma* in greater detail than in the first report (1917); both larvae were referred to the Schistosomatidae. A number of parts of the adult reproductive system were recognized in cell masses present in the body of *C. gracillima*; the nervous system was also described in greater detail than had formerly been done for a furcocercous form. The penetration glands in these two larvae were designated salivary-mucin glands. In discussing the morphology of the different systems of larval trematodes he said (p. 44) of the genital system: "This system of organs has been the most constant basis of classification of adult trematodes. It is also the best specific criterion for the larvae, although a more delicate technic is required for differentiation of the genital organs in the cercaria than in the adult worm." And for the nervous system, he stated (p. 55): "this study has shown that the nervous system of the cercaria is constant for the group to which it belongs, and is a definite basis for the natural classification of the groups." Faust (1918a) described two new forms, *C. gigas* and *C. minor*; the former is peculiarly interesting in its type of excretory system. Cort's (1917) three groups of the furcocercous cercariae were discussed; Faust (p. 108) held that "with the broadening knowledge of schistosome larvae, it seems more reasonable to recognize a complete series of larval forms from those with a pharynx sphincter (*C. douglasi*, *C. emarginatae*, and perhaps *C. vivax* Sonsino), thru those with a degenerate pharynx, with or without intestinal ceca (*C. gracillima*, *C. minor*), thru those without any pharynx, but with well-developed mucin glands (*C. gigas*, *C. tuberistoma*, *C. douthitti*), to the human schistosome cercariae." *C. echinocauda* O'Roke (1917) was also studied and compared with *C. gigas*. In a discussion of the eye-spots in Digenea, Faut (1918b) described those of *C. gigas* in relation to the nervous system.

Cort (1918a) described the excretory system of *Agamodistomum marci*anae, which he held to be the agamodistome stage of a furcocercous cercaria; the development and conservativeness of the excretory system were discussed. Later (1918b) he submitted data to support his thesis that the furcocercous cercariae readily adapt themselves to new molluscan intermediate hosts. Cawston (1918) described *C. secobii* as developing in rediae, although he expressed some doubt as to identification of the species; in previous publications the parthenitae had been reported to be sporocysts. In a later paper (1918a) he recorded a cercaria from the Transvaal with furcae much longer than the tail-stem, for which the name *C. gladii* was proposed. Liston and Soparkar (1918) reported the experimental determination of a furcocercous cercaria as the larva of *Schistosoma spindale* of domestic cattle. Southwell and Prashad (1918) briefly criticized Lühe's (1909) classification of cercariae, because it was based on purely larval structures.

Kobayashi (1918; in Japanese) described a brevifurcate pharyngeal larva with eye-spots, *Cercaria* F, the parthenitae of which were rediae. Cort (1919) described in detail and carefully figured the cercaria of *Schistosoma japonicum*. The most striking difference between this and the previous accounts (Miyairi and Suzuki, 1914; Ogata, 1914) is that three, instead of four, pairs of flame cells were reported for the body; Cort also found two ciliated areas in the distal portion of each bladder arm; all authors have concurred on a single pair of flame cells in the proximal region of the tail-stem. He adopted from Narabayashi the term head gland for the gland contained within the modified oral sucker, and again used cephalic glands to designate the penetration glands. Of these latter glands five pairs were described, in contrast to three pairs reported by Miyairi and Suzuki and by Ogata, and the five or more pairs of Leiper and Atkinson. Cort also included a valuable review of previous publications in the Japanese language. Cawston (1919) briefly described *C. spinosa* from South Africa. In another publication (1919a) he reported finding a small eye-spotted larva for which the name *C. parvoculata* was proposed.

Faust (1919), in a survey of the described cercariae of the United States, recorded the change of name of *C. minor* Faust 1918, preoccupied by Lebour (1912), to *C. minima*. The conservativeness of the excretory and genital systems was discussed, and emphasis laid upon the probable greater value of the latter in the determination of relationships. In a discussion of the excretory system in several groups of the Digenea he proposed (1919c) formulae for the flame cell patterns as found in the cercariae. Brief descriptions of four new species of pharyngeal longifurcate larvae were also included in this paper: three distomes, *C. fuscicauda*, *C. quattuor-solenata* and *C. robusticauda*; and one monostome, *C. rhabdocaeca*. The basic groups of flame cells were taken to consist of either a single flame cell and its capillary, or two or more whose capillaries united and emptied into a larger

excretory tubule. The different groups were represented in the general formula by Greek letters,  $\alpha + \beta + \gamma + \delta + \epsilon$ , five being the largest number of groups present among the ten furcocercous larvae discussed. The simplest condition is in the cercaria of *Schistosoma japonicum*, in which there is a definite division into an anterior group of two,  $\alpha$ , and a posterior group of two,  $\beta$ ; the distinction between anterior and posterior flame cells rests on whether their capillaries empty into anterior or posterior lateral collecting tubules. In the formulae for *C. douthitti* and *C. elephantis* there is the same distinction of  $\alpha$  for anterior and  $\beta$  for posterior groups; while in the Brachycoeliidae, with two anterior and two posterior groups, the primed letters  $\alpha'$  and  $\beta'$  are used for the former and the double-primed letters  $\alpha''$  and  $\beta''$  for the latter, when it would seem clearer from a comparative standpoint to use  $\alpha'$  and  $\alpha''$ , and  $\beta'$  and  $\beta''$ , respectively. Where there is no evident division into anterior and posterior groups, as in the excretory system patterns of the four new species described, Faust used three, four, or five letters to represent the basic groups. *C. emarginatae* and *C. douglasi* (Cort, 1917) were included under the general formula  $\alpha + \beta + \gamma$ , although there is a clear division into anterior and posterior groups.

Faust (1919a) studied Cawston's preserved material of three partly known furcocercous larvae and of the cercaria of *Schistosoma haematobium*; additions were made to the previous descriptions of *C. gladii*, *C. secobii*, and *C. parvoculata*. The description of the cercaria of *S. haematobium* was more complete than any previous one. Three pairs of penetration glands were found, and their ducts, as well as those of *C. gladii*, were described as being capped with hollow piercing spines, structures noted for the first time in connection with glands of cercariae. Material of the cercaria of *S. mansoni* from Venezuela was also studied and the presence of two pairs of granular and four pairs of non-granular penetration gland cells noted; each of the ducts was found to be capped with a hollow piercing spine. The first detailed table for the diagnosis of the human schistosome cercariae was included. Lagrange (1919) very briefly reported a furcocercous cercaria in *Bithynia tentaculata* from France. Iturbe and Gonzalez (1919) published the results of further studies on the cercaria of *S. mansoni* in Venezuela. Four pairs of flame cells were found in the body and one pair in the tail-stem, whereas previously (Iturbe, 1917) five pairs had been reported for the body. Two differentiated sets of penetration gland cells were found and designated as venom and salivary glands; these correspond to Faust's (1919a) granular and non-granular glands.

Sewell (1919) described in detail an apharyngeal larva from India, *C. indica* XXX, which corresponded so closely to the cercaria of *Schistosoma japonicum* that he was not sure of the specific identity of the new form. Instead of the term oral sucker, Sewell employed anterior penetrating organ; the structural modifications from the typical oral sucker of other

larval trematodes had previously been observed in certain furcocercous larvae by a number of workers, notably Looss (1896) and Ssinitzin (1909), but no new term had been used. Lutz (1919), in a paper largely of medical character, used the names *Dicranocercaria ocellifera* and *D. valdefissa* for two larvae; microphotographs were included but no descriptions were given in the text. Porter (1920) studied the cercaria of *Schistosoma haematobium* and noted the presence of three pairs of penetration glands with hollow spines capping their ducts, thus confirming Faust's (1919a) previous observation. She reported finding these cercariae in both *Physopsis africana* and *Lymnaea natalensis*; the latter host genus is new for this larva. The larva of *S. mansoni* was found in three specimens of *Physopsis africana*; this is the first record of this cercaria from a mollusc other than of the genus *Planorbis*. Manson-Bahr and Fairley (1920), in a study of schistosomiasis in Egypt, briefly described the cercariae of *S. haematobium* and *S. mansoni*. They reported the excretory systems to be identical with that described by Cort (1919) for the larva of *S. japonicum*, but also make the conflicting statement that there are "six pairs of flame cells arranged along the margins of the body." Two pairs of large clear penetration gland cells and four pairs of small granular ones were described for the cercaria of *S. mansoni*, and three pairs of large cells with acidophilic protoplasm for the cercaria of *S. haematobium*. Two other furcocercous forms were briefly described and figured, one longifurcate pharyngeal larva (see Manson-Bahr and Fairley 1920, Pl. III, Fig. 7) which appeared to them to be identical with *C. gladii* Cawston, and a brevifurcate form (see Manson-Bahr and Fairley, 1920, Fig. 5), which, although pigmented eye-spots were lacking, they held to be probably *C. bilharziella* Lieper.

Faust (1920), in a consideration of the pathological changes in the snail liver resulting from infestations with larval trematodes, noted the effects of several furcocercous forms, *C. quattuor-solenata*, *C. gigas*, and the cercaria of *Schistosoma mansoni*; the last two species were described as having two kinds of penetration glands, those which are basophilic and those which are eosinophilic. Cawston (1920) reported the presence of a schistosome larva for which he proposed the name *C. crispa*; no detailed description was given. The morphology and bionomics of *C. parvoculata*, *C. gladii* and *C. secobii* were briefly touched upon. Faust (1920a) discussed the criteria for the differentiation of schistosome larvae, recapitulating the most important morphological features and stressing the absence of those characters which had not yet been found in this group. The emphasis earlier placed by him (1918, 1919) on the parts of the developing genital system for the determination of relationships of cercariae was, for the human schistosome larvae, now placed on the number and character of the penetration glands. The distinction was made between the acidophilic or basophilic reactions of the protoplasm, its finely or coarsely granular nature, and the character

of the nuclei. These glands were described and figured for the cercariae of *S. haematobium* and *S. mansoni*. The absence of the head-gland in these two species was also noted.

Scheuring (1920) in a preliminary account reported the experimental determination of the life history of *Sanguinicola inermis* Plehn. This is the first life cycle of a furcocercous cercaria, other than the three human schistosomes and *Schistosoma spindale*, to be worked out in detail. The infective agent was described as a brevifurcate monostome larva which resembled *C. cristata* La Val. St. George. In a survey of Cawston's incompletely described species of cercariae, Faust (1920b) designated *C. spinosa* and *C. crista* as synonyms of the cercariae of human schistosomes, and *C. bilharziellalunata*\* as a synonym of *C. oculata*. Porter (1920a) briefly described the cercaria of *Schistosoma mansoni*, confirming Faust's (1919, 1920) findings of two differentiated sets of penetration glands, two pairs of large anterior cells and four pairs of small posterior cells, all opening through hollow spines which cap the ends of the ducts. *Planorbis pfeifferi* was now reported as the usual host, although *Physopsis africana* also harbors this cercaria. Cort (1921) studied the development of the cercaria of *S. japonicum* in mice; although the indications of sexual dimorphism of adult schistosomes have not yet been described in the cercariae, in this publication and in a subsequent discussion (1921a) on sex in the Schistosomatidae references were made to a species of schistosome cercaria with eye-spots, from Michigan, which exhibited size differences such that Cort interpreted them as sexual dimorphism.

In a paper describing a new blood fluke from turtles, Ward (1921) established the family Proparorchidae and noted that its members are certainly related to the human blood flukes, Schistosomatidae. He also stated that the peculiar blood-inhabiting trematodes belonging to the genera Aporocotyle and Sanguinicola show evident morphological likenesses to the Proparorchidae. Milton (1921), in a paper chiefly of medical nature, severely criticized the nomenclature which had been used by various workers in describing furcocercous cercariae. Kemp (1921) briefly described, from preserved materials only, *Cercaria B* and *Cercaria C*, two brevifurcate forms from Seistan; he also indicated the presence of a larva with extremely long furcae obtained in *Gyraulus euphraticus* in the Hamun-i-Helmand. Faust (1921) added caudal glands to his previous description of *C. quattuor-solenata*.

In a preliminary report of work dealing exclusively with furcocercous larvae of Brazil, Lutz (1921) stated that three new species were found to develop into members of the genus Strigea; for these larvae he proposed the names *Dicranocercaria molluscipeta*, *D. gyrinipeta*, and *D. bdello cystis*.

\* A private communication from Cawston makes clear that this species should be designated *C. bilharziellalunata* nom. nud.

Specific descriptions of them were not given. Soparkar (1921) minutely described the cercaria of *Schistosoma spindale* of India; this is the first account of its structure. Four pairs of flame cells were found in the body and one pair in the tail-stem, while the penetration gland equipment was found to consist of four anterior coarsely granular cells with acidophilic protoplasm, and six posterior in which the finely granular protoplasm is basophilic. A detailed table of comparison of the three human schistosome larvae, of the larvae of *S. spindale*, and of *C. indica* XXX was given; the most extensive summary yet made of the common characters of the human and animal schistosome larvae was also included. The term Schistocercaria was proposed for the furcocercous cercariae whose identity with adult schistosomes has been established. Soparkar (1921a) also described in detail four new furcocercous larvae from India. One of these, *C. bombayensis* no. 8, is especially interesting in that it appears to be a connecting link between the monostome and distome groups of the brevifurcate apharyngeal cercariae; development takes place in typical rediae which arise from small sporocysts. Details of the morphology of *C. bombayensis* no. 9, a pharyngeal distome larva, and of *C. bombayensis* no. 13 and no. 19, apharyngeal distomes, were presented, with figures showing the principal systems. Faust (1921d) described *C. octadena*, a brevifurcate pharyngeal distome larva, from preserved material, and added notes on another South African form, *C. secobii* Cawston 1915. In this paper he suggested that cephalic gland (Cort 1919) is a more suitable term than mucin gland (Faust 1918). Porter's (1921) studies on the larvae of *Schistosoma haematobium* and *S. mansoni* confirmed Faust's earlier work (1919a, 1920a) on the morphology of these forms, as well as her own previous findings (1920, 1920a). Yet a third genus of molluscs was said to harbor the cercaria of *S. mansoni*; a single infected specimen of *Isidora tropica* was found.

Khalil (1922) presented a structural analysis of the cercaria of *S. mansoni* based on a study of living material. His report of three pairs of flame cells in the body, together with two pairs of ciliated areas in the lateral excretory ducts, differs from most previous accounts; the larger numbers observed by other authors may be accounted for by the assumption that they have mistaken the ciliated areas for flame cells. Thus the excretory system pattern agreed essentially with that of the only other human schistosome larva for which it was known at that time, the cercaria of *S. japonicum*, according to Cort (1919). Khalil adopted Milton's (1921) designation of peri-acetabular glands for the penetration glands; a posterior set of three pairs was reported, although Faust (1919a, 1920a), confirmed by Manson-Bahr and Fairley (1920) and by Porter (1921), had described four posterior pairs; all agreed on the presence of two anterior pairs. Milton (1922), from an incomplete study of the literature, attempted to show that measurements could be used as the basis of diagnosis of the furcocercous cercariae.



The proposed system is too artificial; furthermore, he incorrectly took measurements from descriptions, assigned confusing specific names, and made misstatements concerning structures the original descriptions of which were clear. Bettencourt and da Silva (1922) described in detail the structure of the cercaria of *S. haematobium*, from snail hosts naturally infested in Portugal. Theirs is the first authentic account and figure of the excretory system pattern which agrees essentially with that for the cercaria of *S. japonicum* by Cort (1919) and of *S. mansoni* by Khalil (1922).

Cort (1922) studied the escape of cercariae from their snail hosts, using *C. elephantis* emerging from *Planorbis trivolvis* for most of the data. Wide variation was found in the numbers escaping from different molluscs; temperature was shown to be a factor in the regulation of the number from any one snail. Furthermore, the cercariae of this species emerged in regularly recurring waves, once during the twenty-four hours, the time of the wave differing in different hosts.

Sewell (1922), as a result of comprehensive studies of the larval trematode fauna of India, described a large number of new species, of which fourteen were furcocercous forms; he included the first complete survey of all furcocercous cercariae. The lead of Lühe (1909) in considering separately the monostome (Lophocercariae) and the distome (furcocercous) forms was followed, and the composite nature of the latter group was clearly recognized. Practically all of the known furcocercous forms were considered; seven larvae, some of which were incompletely described, could not be included in his groupings. In considering the excretory system pattern he used formulae modified from those devised by Looss (1894:68), and used by Cort (1919b) in the description of a stylet cercaria. Further consideration of Sewell's classification is included in that section in the present paper. He also took up Faust's (1918:108) discussion of the distome larvae, in which a graded series of furcocercous cercariae in the family Schistosomatidae was recognized, from larvae with a muscular pharynx through those with a degenerate pharynx to the apharyngeal forms. This view was strongly contested as being too inclusive, practically making the terms furcocercous and schistosome synonymous. In addition to detailed descriptions of fourteen new furcocercous cercariae, Sewell described the miracidia of *Schistosoma haematobium* and of *C. indica* XV; he found that the sporocysts producing this latter species have in addition the remarkable power of giving rise to miracidia. He discussed the value of the excretory system pattern in the miracidium and in the sporocyst and redia, and used these data in his tables showing relationships between the various subgroups of monostome and distome larvae. In discussing the line of evolution and development of the furcocercous forms, he presented data to show that the *Lophocerca* and the *Lophoides* groups of monostomes are closely related to his Groups 1 and 2, respectively, of the distome larvae, and that

within each of the distome groups the sub-groups could be arranged in progressive series. Unfortunately, these gradations are in part based on errors, due to incomplete and incorrect details of descriptions of other authors.

Kobayashi (1922) reviewed the accounts of the cercariae from Japan, Formosa and Korea which had been published in the Japanese language; brief descriptions of the furcocercous forms were given, one of them new. No specific names had been ascribed to most of these, although the original authors had designated them by numbers or letters. Kobayashi renamed the ten species by letters from A through J, and gave sketches for three of them. Ruzskowski (1922), in a study of the life history of *Hemistomum alatum*, very briefly described the longifurcate distome cercaria which he obtained from experimentally infested snails. Scheuring's (1922) complete report of the life history of *Sanguinicola inermis* described in greater detail the brevifurcate monostome cercaria, whose identity with *C. cristata* is held by him to be doubtful; the excretory system pattern was not reported. Cawston (1922c), in a note on the differentiation of certain schistosome cercariae, suggested the probable synonymy of *C. crispa* Cawston with the cercaria of *Schistosoma haematobium*. The report of Bettencourt and Borges with de Seabra and da Silva (1922), on the study of schistosomiasis in Portugal, included a description of the cercaria of *S. haematobium* and a discussion of the nomenclature of furcocercous larvae. They found what was thought to be a head gland; Faust (1920a) stated that this organ is present only in the cercaria of *S. japonicum* among the human schistosomes. Brumpt (1922) incidentally mentioned a furcocercous larva, closely allied to *C. fissicauda*, as being the larva of a holostome of the genus *Tylodelphis*.

Faust (1922a) described in detail *C. leptoderma*, a larva which has the same type of excretory system as has *C. vivax*. This new species is the first furcocercous larva in which the development of this system, including the number of flame cells, has been followed from its first appearance in the germ ball to the stage of development found in the mature cercaria; the observations of Looss (1896) on *C. vivax*, while otherwise complete, did not make clear the numbers and arrangements of the flame cells. On either side of the elongating germ ball of *C. leptoderma* the division of the single flame cell establishes the fundamental anterior and posterior groups,  $\alpha + \beta$ ; then follows a trichotomy of both  $\alpha$  and  $\beta$  elements, followed by a trichotomy of each of the resulting cells, which results in eighteen flame cells on either side of the mature cercaria. The complete formula was taken as  $(\alpha)^2 + (\beta)^2$ , with three indicated as the factor to represent two successive trichotomies.

In a preliminary publication on the development of trematodes of Brazil, Lutz (1922) reported having observed a dozen species of furcocer-

cous larvae, many of which he found to belong to the holostomids, with at least one schistosome. Faust and Meleney (1923) published a brief summary of their work on the life history of *Schistosoma japonicum* which later (1924) appeared in an extensive monograph. Tanabe (1923) described a furcocercous cercaria which he found to develop in experimentally infected mice into a new schistosome, to which he assigned the name *Schistosomatium pathlocopticum*. The larva, which is an apharyngeal brevifurcate distome, very closely resembles *C. douthitti* in general appearance and proportions, and agrees with it in the details of the excretory and digestive systems; it has only three pairs of penetration glands, whereas *C. douthitti* has five pairs. Infection of mice was shown to be through penetration of the skin by the cercariae.

Lagrange (1923), in a study of larval trematodes from Indo-China, described two furcocercous cercariae; no specific names were given and there are no figures. One species, *Schistosoma?*, is a distome and is probably apharyngeal; from the measurements given, it is a longifurcate cercaria, and none of the human schistosomes are longifurcate. The other larva is a brevifurcate distome, but there is no indication whether a pharynx is present; it is one of the few furcocercous larvae which develop in rediae. Miller (1923), in a publication preliminary to the present paper, described seven new species of North American larvae, two apharyngeal brevifurcate distomes, and five longifurcate forms, probably all pharyngeal, of which two were monostomes. A classification of the apharyngeal and pharyngeal brevifurcate distomes was presented; a key, based largely on data obtainable only from living cercariae, was given to separate the groups. Stunkard (1923) described a number of new blood flukes from turtles and discussed the relationships of the Aporocotylidae from fishes, the Spirorchidae from turtles and the Schistosomatidae from birds and mammals. He came to the conclusion that the blood flukes constitute a natural group. The larvae of some, and presumably all, members of the first and last families are furcocercous cercariae, and in view of other similarities it might be expected that the Spirorchidae would also develop from apharyngeal furcocercous larvae.

McCormick (1923) studied the larval trematode parasitization of seven species of fresh water snails from Ohio. He reported finding *C. echinocauda* and *C. gracillima*; the present author, from an examination of mounted material, believes that the identification of the latter species is doubtfully correct. Hesse (1923) described in detail a furcocercous cercaria from *Lymnaea peregra* in Scotland. No specific name was given; the larva is a pharyngeal, longifurcate distome, with seven pairs of flame cells in the body and two pairs in the tail-stem; there are four penetration gland cells. Sophrakar's (1924) detailed description of a unique furcocercous form from India shows it to be an apharyngeal distome larva in which the genital

system is much more highly developed than in any previously reported form; testes and ovary are present and active spermatozoa were found. The excretory system is highly developed, with forty flame cells around the margin of the body; the capillaries were not traced. The tail-stem is unique in the presence of two short cross arms, proximally located; three pairs of flame cells empty directly into the caudal excretory tube. The intestinal ceca are united in the posterior part of the body. Development of this species takes place in rediae.

Szidat (1924) described three pharyngeal longifurcate distomes from Prussia; they were not given specific names, but were designated as *Cercaria A*, *Cercaria B* and *Cercaria C*. The question of the identity of *Cercaria B* and *C. gracilis*, and of *Cercaria C* and *C. letifera*, *C. furcata* and *C. fissicauda* was raised by Szidat, who felt that the incompleteness of the earlier descriptions made a decision impossible. Following penetration of *Cercaria A* into *Lymnaea palustris* and its migration to the hermaphrodite gland, its development into *Tetracotyle typica* Diesing was traced and several stages were figured. This is the first demonstration of the post-larval development of a pharyngeal furcocercous cercaria, although the preliminary report of Lutz (1922) indicated that similar results had been obtained with three South American forms.

Faust and Meleney (1924) published a large monograph on oriental schistosomiasis, in which the results of their extensive studies from both the medical and zoological aspects were presented. They reported the results of much experimental as well as observational work which they had carried out on different phases of the life cycle of *Schistosoma japonicum*, and included a valuable review of the important literature, most of which had hitherto been practically inaccessible, since it is in Japanese. Their most important contribution to the knowledge of the cercaria is a study of the excretory system development in five stages,  $\alpha$ - $\epsilon$ , of the schistosomulum. It was found that the loss of the tail-stem flame cells is compensated by the early division of the other flame cells draining into the posterior collecting tubules. In the  $\gamma$  stage a division of each of the flame cells has taken place, so that there are eight in either lateral half of the body; a further dichotomy has taken place in the  $\epsilon$  stage, resulting in a total of thirty-two flame cells for the entire body. These stages show the method of systematic elaboration of the flame cell pattern in the cercaria to the excretory system of at least the young worm, and presumably on to the adult schistosome. This is the first record of excretory system development in a number of the post-larval stages of a furcocercous cercaria. Faust (1924), in a further study of larval flukes from China, described three furcocercous forms, *C. pseudo-vivax*, *C. divaricata*\* and *C. gigantea*. The first two are pharyngeal longifur-

\* This larva is listed in his Table I, page 296, and in Table II opposite page 298 as *C. divaricauda*; the specific description on page 256 is headed *C. divaricata* nov. spec.

cate larvae; although the alimentary canal of *C. gigantea* is unknown, in other respects it rather closely resembles *C. bombayensis* no. 19, and is probably apharyngeal. It is surprising that the three new larvae are included under the family Schistosomatidae, especially the two which have definite pharynges; it would seem that Faust has not taken cognizance of the work of Ruszkowski (1922) and Lutz (1922) on the life histories of holostomes, all of which, so far as known, have furcocercous pharyngeal larvae. Faust also considered all previous descriptions of larval trematodes from the Sino-Japanese regions, and assigned specific names to the cercariae reviewed by Kobayashi (1922). The most important part of the paper deals with the systematic grouping of larval and adult trematodes; this will be discussed in detail in this paper under the heading of Classification.

Miller (1924) studied *C. douthitti* and showed that it has most of the typical characters of the schistosome larvae; Cort's description was emended in certain particulars. Studies on co-type material of *C. echinocauda* showed that a very large posterior cell mass of unknown function is present, as are two differentiated sets of penetration gland cells; a head gland and an alimentary canal similar to that of *C. elvae* were also described. Similarities of *C. echinocauda* with *C. elephantis* were noted. Blacklock and Thompson (1924) described the cercaria of *Schistosoma haematobium* from both living and preserved material obtained from *Physopsis* cf. *globosa* in Sierra Leone. Their account differs strikingly from the descriptions of Faust, of Bettencourt and da Silva, and of Bettencourt, Borges et al in the number and character of the penetration glands. Instead of three pairs of similar glands, they report two pairs of large anterior cells containing coarsely granular protoplasm, and three pairs of smaller posterior cells which are finely granular. Except when overwhelmed with stain, the anterior cells are eosinophilic, and the posterior are basophilic to Ehrlich's hematoxylin; "the results obtained by staining were, however, not constant, even in fully developed cercariae." (p. 218). These authors critically surveyed the descriptions of the three human schistosome cercariae and severely attacked the work of Faust on the cercariae of *S. haematobium* and *S. mansoni*; they have either not seen or have ignored the work of Manson-Bahr and Fairley and of Porter which confirmed Faust's descriptions (in details) with respect to gland numbers in these two species. In support of their view that they are dealing with the cercaria of *S. haematobium* is the epidemiological evidence of the presence of the urinary schistosomiasis of this trematode and the absence in Sierra Leone of the intestinal type caused by *S. mansoni*. Furthermore, they found this cercaria in no other host than *Physopsis* sp., the genus in which the larva of *S. haematobium* in Africa has usually been found. They also reported the recovery of adult males morphologically identical with *S. haematobium*, from guinea pigs and monkeys experimentally infected with the cercaria described.

Their account of the experimental infection of *Physopsis* cf. *globosa* with miracidia, hatched from terminal-spined eggs from the urine of an infected case, is less conclusive, fifteen days, judging from the life history of *S. japonicum*, is much too short a period for the development of the miracidium through the parthenogenetic generations to mature emerging cercariae. Only nine snails were used, and of these three were later found to be infected; the statement that "controls which were dissected did not show any infections" does not indicate the number used. It seems likely that the three experimental snails harbored natural infections which, in one case, resulted in emerging cercariae on the fifteenth day. These cercariae developed in monkeys into adult males of *S. haematobium*.

In a short paper written after studying Khalil's (1922) description of the cercaria of *S. mansoni* and the account of the cercaria of *S. haematobium* by Bettencourt and da Silva (1922), Blacklock and Thompson (1924a) discussed the close morphological correspondence of their species with that described by Khalil from Egypt as the cercaria of *S. mansoni*. On the contrary, there is variance with the description of the cercaria of *S. haematobium* (Bettencourt and da Silva) from Portugal. Blacklock and Thompson conclude that if the glands of the cercaria of *S. japonicum* are constantly of one type this species may be differentiated from the other schistosome larvae; but that the cercariae of *S. haematobium* (as described by them), of *S. mansoni* (according to Khalil), and *C. indica* XXX are without significant morphological differences. They discuss the possibility of classification by intermediate host; the only well established case of the cercaria of *S. haematobium* in a mollusc genus other than *Physopsis* (Bullinus), that of Bettencourt et al in which *Planorbis metidjensis* in the sole carrier in Portugal, seems to them to make it impossible to identify the human cercariae by this means. This view is supported by the work of Porter (1920a, 1921), apparently unknown to them, in which the cercaria of *S. haematobium* in South Africa was found in both *Physopsis* and *Lymnaea*, and the cercaria of *S. mansoni* was found in *Physopsis* and in *Isidora* as well as in the usual host *Planorbis*.

#### METHODS OF INVESTIGATION

The emphasis laid upon the study of living material by Cort, Faust, Soparkar, Sewell and others is well placed, and the essentials of the method as outlined by Cort (1918c, 1919, 1922) were followed by the author in the study of the structure of all forms. At the beginning of the investigation in 1920 all snails of a collection were crushed to obtain the cercariae and parthenitae. The limitations of this method led to the adoption of the isolation of snails; this was done in suitable glass vials in a small amount of water; if mature cercariae are present they usually emerge from the body of the snail within twenty-four hours and may be detected easily with the

naked eye, or with a hand lens. By transference to a small aquarium the infested snail may be kept alive for some time, and a supply of living mature cercariae is made available by periodic confinement to a small amount of water in a vial. The exact percentage of infestation was determined by crushing all snails from which larvae were not emerging after forty-eight hours' isolation. For the preparation of total mounts the mature cercariae were fixed by pouring them into a large amount of warm fixing fluid; Gilson's mercurio-nitric, corrosive-acetic, saturated aqueous corrosive sublimate, and Bouin's fluid were used. Only such material was the basis of the measurements recorded.

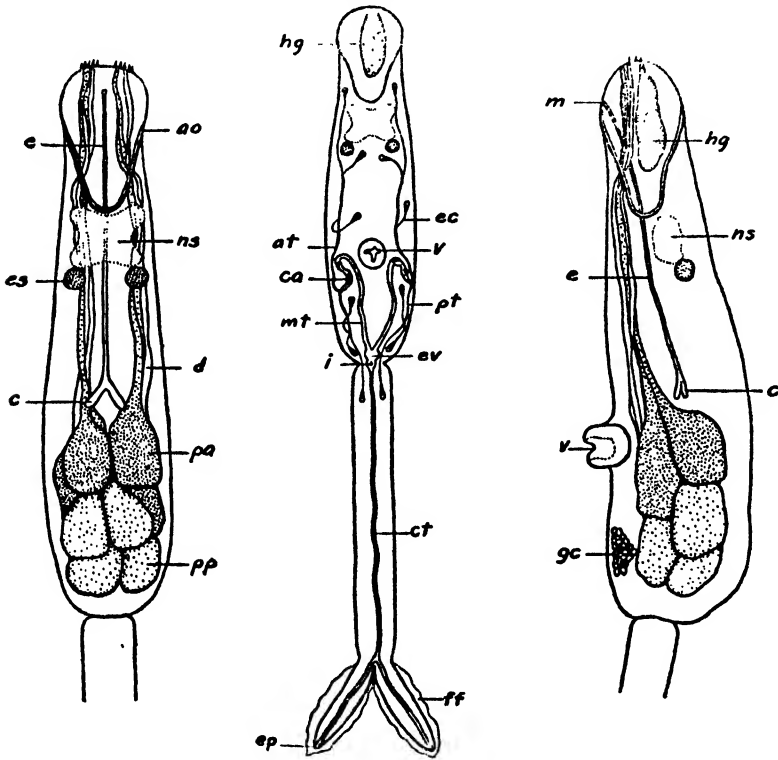
When no more living cercariae were needed, the snail was crushed and a portion of the infested tissue was carefully dissected, and the young stages and living parthenitae were studied; permanent mounts of these were also made. The study of immature larvae is an important phase of the work on structure, as certain parts are relatively more easily seen than in mature larvae. A portion of the infested organ, which is usually the digestive gland, was fixed for sectioning. Sections were cut four to five  $\mu$  in thickness, and stained with various standard stains. The mounting media employed were Canada balsam and, for total mounts, white or green Diaphane. Studies were also made of temporary mounts in various oils, and in glycerine and glycerine-and-water media, in order to secure different refractive indices. Intra-vitam staining with neutral red proved very useful in the definition of certain glands and organs, and in inhibiting the activity of the larvae.

#### NOMENCLATURE

The lack of agreement in the nomenclature of certain organs in the furcocercous cercariae makes it desirable to establish uniformity for future descriptions. A brief account of structure is presented here, based on an apharyngeal brevifurcate distome larva (Text-fig. 1); the various departures from this type which are found in the different groups are included in the discussion.

The structure here designated as anterior organ (*ao*) is a modified oral sucker, which Sewell (1922) called the anterior protrusible penetrating organ. Its poor powers of attachment, and the difference in the mechanism of ventral sucker (*v*) and anterior organ have been recognized by a number of investigators, although many recent ones retain the term oral sucker. The organ is differentiated into a thin-walled anterior part and a thicker walled posterior part in the brevifurcate larvae; this differentiation is lacking in many of the longifurcate forms. However, the anterior organ seems always to be protrusible and invertible, and represents an oral sucker modified for penetrating tissues. Cort (1919:498) is followed in the use of head gland (*hg*) for the group of cells designated by Narabayashi as Kopfdrüse, which are dorsally located within the anterior organ. As this struc-

ture has no connection with the mouth, the term oral gland proposed by Khalil (1922) is not suitable. The head gland is present in most known schistosome larvae, and possibly in all other brevifurcate forms. In several longifurcate larvae two or more cells, similarly located, have been reported; the author suggests no term for these cells; they can not be designated properly until it is known whether they are homologous with the head-gland of apharyngeal brevifurcate cercariae.



Text-fig. 1

The oral cavity is seldom more than a capillary tube through the anterior organ. An esophagus (*e*) and a single cecum, or pair of ceca (*c*), constitute the remainder of the simple alimentary canal. In the majority of longifurcate larvae and in three brevifurcate forms, there is a pharynx at a variable distance behind the anterior organ; in these cases, following the nomenclature for adult trematodes, the portion of the alimentary canal between the pharynx and the anterior organ is called the prepharynx.

A pair of pigmented eye-spots (*es*) may be in connection with the nervous system (*ns*); these are called simple eye-spots when they are composed of a small, but varying, number of pigment granules of different shapes and sizes, and compound eye-spots when there are numerous uni-



formly fine granules, arranged as a cup within which may often be seen a lens. Unpigmented eye-spots have been reported.

The large unicellular glands, usually in the middle and posterior parts of the body, have been variously designated as salivary, poison, cephalic, digestive, mucus, mucin, salivary-mucin, peri-acetabular and secretory glands. In one group (*Vivax*) they are located only toward the anterior, and even within the anterior organ. The confusion caused by this multiplicity of terms has been considered by Sewell, who adopted salivary gland, first used by Ssinitzin (1911) for *C. discursata*. The author does not consider this a suitable designation, as the term salivary gland has, in all groups of the animal kingdom, been used in connection with the alimentary canal. Neither is the frequently used term cephalic gland satisfactory, as it would seem to imply an anterior location, and also it is too similar to head gland, which signifies an altogether different structure; mucin gland implies a definite chemical nature, and it is not certain that mucin is present in these cells. All evidence shows that these glands are concerned with the dissolution of host tissue; in the mammalian schistosomes and in certain holostomes a number of authors, including Faust and Meleney, and Szidat, have demonstrated that these glands disappear soon after penetration of the skin of the definitive or intermediate host, and chiefly for this reason the present author has designated them as penetration glands. This term most nearly expresses the known function of the glands, and does not refer them to any definite position within the body; their location varies considerably in the different groups of furcocercous cercariae. In the brevifurcate distome larvae there may be a differentiation of the penetration glands into two sorts: anterior coarsely-granular glands (*pa*) which are oxyphilic in sections, and posterior finely-granular glands (*pp*) which are basophilic.

Various authors have designated as either ovary or testis the mass of germ cells (*gc*); it does not seem safe to venture a prediction as to the adult organ represented, except where the rudiments of all parts have been recognized, as by Faust (1918) in *C. gracillima*.

The nomenclature for the parts of the excretory system has been compiled from that used by Looss, Cort, Faust and Sewell. The posterior median bladder, or excretory vesicle (*ev*), has two lateral arms which may pass anteriorly with gradually diminishing caliber or which may be tubes of uniformly much smaller diameter than is the excretory vesicle itself. Cort considers these lateral arms as parts of the bladder, while Faust, Soparkar and Sewell have designated them as main collecting tubes, main excretory tubes, and main lateral collecting tubes (*mt*); Sewell's usage of the latter term has been accepted here. Into each main lateral collecting tube there usually pours an anterior collecting tubule (*at*) and a posterior collecting tubule (*pt*). Further subdivisions into capillary tubules (*ec*) lead

to the flame cells. The Vivax group, the members of which have a highly developed excretory system, have, in addition to the lateral collecting tubes, a median collecting tube which joins with a branch from each of the laterals at its anterior end, and which divides toward its posterior end before entering the excretory vesicle (see *C. leptoderma* in Faust, 1922a). In some cercariae there are cilia in one or two places in the main lateral collecting tubes; the term ciliated area (*ca*) has been used in describing these (Cort, 1919). Although, as figured by different authors, the cilia may be in a compact tuft or may project independently into the lumen (in the cercaria of *Schistosomum japonicum* only, as figured by Cort, 1919), this term may be used to designate either type of ciliation. It may be noted here that these structures are seen only in the instant before a cercaria goes to pieces due to cover glass pressure. At the junction of body and tail, the excretory vesicle joins the caudal excretory tube (*ct*), usually with a small protoplasmic island at the place of union. The studies of Looss (1896) on the development of *C. vivax* revealed this as a remnant of the embryonic paired condition of the caudal excretory tube; Faust (1917) termed it an eyelet anastomosis, and later (1919c) the island of Cort (*i*), which latter designation the present author has used.

In some species the bifurcations of the tail are less than one-half the stem length, while in others they are equal to and in some cases longer than the tail-stem; both the pharyngeal and the apharyngeal larvae are subdivided partly on this basis into brevifurcate and longifurcate groups. The caudal excretory tube bifurcates with the tail, and in brevifurcate larvae the branches open at the tips of the furcae (*ep*); in other cases the openings are somewhere along the edge, usually midway of the furcae. In some cercariae the furcae may be laterally flattened, and in addition provided with a dorso-ventral extension of the cuticula; this furcal fin-fold (*ff*) may be narrow or wide, and in the latter case it is usually fluted. It has also been called cuticular keel and paddle edge.

## DESCRIPTION OF SPECIES AND COMPARISON WITH RELATED FORMS

APHARYNGEAL BREVIFURCATE DISTOME CERCARIAE

### CERCARIA ELVAE MILLER 1923

[Figs. 19-28, 38-42]

Host, *Lymnaea stagnalis* var. *appressa*

Locality, Douglas Lake, Michigan (Hook Point and Bessey Creek)

Occasion, twice, in July and August, 1921

This cercaria is similar to those of the family Schistosomatidae in a number of characters. It is most closely like *C. bombayensis* no. 19, which was found once in *Lymnaea acuminata* from Bombay by Soparkar (1921a: 30), who noted that it probably belonged to the "Bilharziella" group of cercariae. The description of *C. ocellata* La Val. St. George which was given by Ssnitzin (1909:314), although incomplete in some important details of the excretory system, indicates close relationship of *C. elvae* to this form also. *C. gigantea*, recently found by Faust (1924) in China, is most closely similar to *C. bombayensis* no. 19.

The behavior is strikingly like that of the larvae of the schistosomes which have been studied in this particular. The emerged cercariae sink slowly through the water with body down and furcae 60° to 80° apart, and with tail-stem generally straight; occasionally the body is somewhat re-curved upon the tail. Swimming is effected by a rapid lashing of the tail, with either body or tail in advance; the latter is more frequent. Both beginning and cessation of locomotion are abrupt and the direction is usually erratic; there is probably less locomotion in a straight line than Soparkar (1921) reported for the cercaria of *Schistosoma spindale* and the author found in *C. wardi*. The inchworm locomotion described for the cercariae of *Schistosoma japonicum* by Cort (1919) and of *S. spindale* was observed in numerous specimens of *C. elvae*; under a cover glass it takes place as follows: after extension of the body, the anterior organ takes hold of the substratum, the body is contracted, and the posterior part is rotated through about 80°; the ventral sucker, which therefore protrudes laterally, is placed beside the anterior organ and takes hold of the substratum; the attachment of the latter is now released, and the series of movements is repeated. The intermittent lashing of the tail which occurs is not definitely correlated with either extension or contraction of the body. After decaudation, which takes place easily in this species, the animal is able to progress by the method just described, but not so readily as before. Sewell noted for *C. indica*

XXX, apparently a true schistosome, that there was a marked tendency to shed the tail while under observation. This organ, when detached, continues in erratic locomotion for some time. When the larva is at rest, or practically so, the furcae are often held at right angles to the tail-stem.

There are several additional points of behavior under a cover glass to be noted. The animal takes hold of the substratum with its anterior organ and makes slow, jerky movements of the body; or body and tail are held in a straight line, somewhat rigid, and then rapidly bent in the middle to one side and the other several times. Often there are rapid vibrations of the tail, such that the animal is spun around on the anterior organ as a pivot; less frequently, the ventral sucker is attached and acts as the center of turning through an angle of less than  $180^\circ$ , but, due possibly to the large size of this form and consequent greater pressure of the cover glass, there is no complete spinning about, such as was reported by Cort (1915:50) for *C. douthitti* from *Lymnaea reflexa*, and has been observed by the present author for the same form from *L. stagnalis* var. *appressa* when studied under a cover glass.

Sizes under various conditions are: maximum extension when living, body  $368\ \mu$  by  $80\ \mu$ , tail-stem  $501\ \mu$ , furca  $328\ \mu$ ; well-extended specimens mounted in Canada balsam (average), body  $368\ \mu$  by  $41\ \mu$ , tail-stem  $382\ \mu$ , furca  $290\ \mu$ . Although both *C. bombayensis* no. 19 and *C. ocellata* are larger than *C. elvae*, the proportions in length of body, tail-stem, and furcae remain practically constant; the tail-stem is somewhat longer than the body, which in turn is longer than the furcae. *C. gigantea* is smaller than any of these three.

*C. elvae* is very transparent; the deeply pigmented eye-spots stand out in sharp contrast to the hyaline body of the living animal, and the thick ducts of the penetration glands are very prominent structures, especially from the region of the eye-spots forward and through the anterior organ. The spindle-shaped body tapers more gradually from the ventral sucker toward the anterior end than toward the posterior; it is the contraction and extension of the anterior part of the body which cause the great changes in length. Because of the protruding ventral sucker a frontal mount is difficult to obtain, and the cercaria is usually seen lying on its side, in which position practically all observations must be made.

The entire surface is evenly and finely spined; Soparkar showed a like condition for *C. bombayensis* no. 19. For *C. ocellata*, sensory hairs were reported on the body and ends of the furcae; it is possible that Ssinitzin mistook the flutings of the furcal fin-folds for hairs, as O'Roke did later on *C. echinocauda* (1917); the latter error was corrected by Faust (1918a). *C. gigantea* is spined on body, tail-stem and furcae.

The anterior organ is large, and occupies the entire anterior third of the body; the length in mounted specimens averages  $96\ \mu$ . Its shape is

pyriform in the living animal, with the small end posterior (Fig. 22), and elongate-oval or dumb-bell shape in mounted cercariae. The walls of the posterior part are strongly muscular (Fig. 28) as in the known schistosome larvae, and as in *C. ocellata* and in *C. bombayensis* no. 19. The anterior part is thinner (Fig. 26), especially toward the foremost part which is, as Cort reported for the cercaria of *Schistosoma japonicum*, in direct contact with the cuticula (Fig. 27); the same condition is present in *C. ocellata* and *C. bombayensis* no. 19. The head gland is conspicuous in the anterior organ; its size varies, but it never extends far into the posterior muscular part. It appears coarsely granular in the living animal and is strongly eosinophilic in sections. Ssinitzin observed in *C. ocellata* what was probably a head gland; such an organ is present in *C. bombayensis* no. 19 and in *C. gigantea*. Whether it consists of one cell or many has not been definitely determined. Large nuclei are seen in both total mounts and sections; it could not be observed whether they are enveloped by the head gland wall or merely pressed against its surface. Cort noted for the cercaria of *Schistosoma japonicum* that "a layer of large nuclei surround the gland and are evidently a part of it." Soparkar, in his description of the larva of *S. spindale*, was less confident of the relations, and stated that "it is surrounded by several nuclei, but these do not seem to be a part of the gland." The opening is on the extreme anterior end, slightly dorsal.

The ventral sucker is prominent; it has a diameter of about  $33\ \mu$  in living larvae and averages  $23\ \mu$  in specimens mounted in Canada balsam. There are at least two sets of muscle fibers: circular ones are especially prominent around the non-nucleated distal part (Fig. 21), while powerful bands radiate from the proximal region to parts of the dorsal side of the body, where they are inserted. These bands are very clearly seen in the living animal and are more striking structures in this cercaria than in any other form observed by the author.

The powerful tail is attached terminally to the body; it is about as wide as the body at its proximal end and diminishes slightly toward the end where the two furcae arise. These are not so sharply delimited as in the larvae which are known to be true schistosomes, but represent an intermediate condition between them and the longifurcate forms. The furcae of *C. ocellata* are shown with constrictions at their bases by both La Valette St. George and Ssinitzin; Soparkar does not so figure them for *C. bombayensis* no. 19. There are four large bands of longitudinal muscles, and two small ones which apparently consist of but one fiber each (Fig. 23). The furcae are somewhat laterally compressed.

The eye-spots of *C. elvae* are compound; each is a cup, composed of fine brownish granules, within which a lens is found (Fig. 39). The average measurements are  $8\ \mu$  wide and  $5\ \mu$  deep, and the greatest diameter of the protruding lens is about  $5\ \mu$ . It is evident that the same type of eye-spot is

present in *C. bombayensis* no. 19; Ssnitzin's account for *C. ocellata* is not absolutely clear on this point; Faust described a pair of pigmented eye-spots in *C. gigantea*, as well as pigmentation on the body.

The type of alimentary canal is similar to that found in the schistosomes, with a small ventral mouth, a capillary esophagus through the anterior organ (Fig. 28), penetrating its wall in the posterior median region, and continuing (Fig. 41) to bifurcate into short ceca. In the cercariae of *Schistosoma japonicum* and *S. spindale* the ceca are represented as heart-shaped, somewhat variable; at the most they are short dilated diverticula. In both *C. elvae* and *C. ocellata* they are short and straight (Fig. 20), differing only in length from those of *C. bombayensis* no. 19, in which they are curved partly around the ventral sucker, terminating at about its middle. The difficulty of observing the presence of the mouth and oral tube, especially in preserved material, is considerable, even with a magnification of 1380 diameters; Ssnitzin noted the same difficulty in *C. ocellata*. Faust was unable to find an alimentary canal in *C. gigantea*. No trace of a pharynx is found in any of these forms.

The main part of the nervous system is represented by a bilobed mass which lies just anterior to the eye-spots, in connection with it (Fig. 19). In *C. bombayensis* no. 19 two large lobes lateral to the penetration gland ducts were observed, without a cross-connection; in *C. elvae* the penetration gland ducts of each side pass directly under the ganglionic mass (Fig. 41). These ducts are median to the lobes of the nervous system also in the cercariae of *Schistosoma spindale* and of *S. japonicum*.

The penetration glands occupy a great part of the body, almost the entire posterior half of *C. elvae*, and even a considerably greater portion of *C. ocellata*. Furthermore, there is a definite distinction in each between an anterior and a posterior group of cells. On the contrary, these glands in *C. bombayensis* no. 19 and *C. gigantea* are less prominent structures, and no distinction of two sets is shown. Under low magnification, the body and tail of *C. elvae* are transparent, and slightly yellow in color, with the exception of the greater part of the body posterior to the ventral sucker, which is a clear light gray. Around the ventral sucker there is a yellow, more granular area representing the anterior set of penetration glands (Fig. 25). The number and relation of the cells within each group are not easily determined in the living animal, due to their transparency and contiguity, and it is only under magnification of about a thousand diameters that the outlines are visible. There are three pairs of clear grayish glands in the posterior part of the body and two pairs of circum-acetabular glands with more granular contents; of the latter one is anterior and the other posterior to the ventral sucker. In unstained specimens mounted in Canada balsam the grayish glands become very dark and stand out in marked contrast. The ducts from these five pairs of cells run forward in a bundle on

each side, most prominent just anterior to the eye-spots. In lateral view of the living animal there are two yellow granular ducts from the anterior cells, dorsal to an apparently single transparent grayish duct; this latter is composed of three which drain the posterior cells (Fig. 39). Both cells and ducts of the two groups differ in staining reactions; the posterior take a very deep stain with Delafield's hematoxylin and then appear coarsely granular; the anterior are practically chromophobic to both hematoxylin and the eosins, and the greater part of the contents appears to have been discharged, or dissolved out at some stage in the preparation.

*C. ocellata* and *C. elvae* are not quite identical in their penetration gland equipment; the fact that *C. bombayensis* no. 19 and *C. gigantea* have only one set of four pairs of similar cells does not, in view of other characters, preclude their being placed with these two. For, among the larvae which are known to be schistosomes, the cercariae of *Schistosoma japonicum* and *S. haematobium* were described as having only one group of acidophilic glands, while Faust (1920a) showed that even in the immature larva of *S. mansoni* two sets have been differentiated, the anterior composed of four coarsely granular acidophilic cells, and the posterior of eight, smaller and basophilic. Soparkar definitely described the ends of the penetration gland ducts in *C. bombayensis* no. 19 as being capped with hollow piercing spines; in *C. elvae* spines are present, but whether they are hollow was not definitely determined. Ssinitzin did not record their presence in *C. ocellata*, and Faust made no mention of them in *C. gigantea*.

The details of the excretory system were worked out in the living animal (Fig. 20). There are six pairs of flame cells in the body; three on each side empty into the anterior, and three into the posterior collecting tubule. There is a seventh pair in the proximal region of the tail-stem. There is practical identity with *C. bombayensis* no. 19, with only minor differences such as locations of flame cells and length of tubules. The excretory vesicles are of the same type; and an island of Cort is present at the junction of body and tail. The caudal excretory tube bifurcates at the origin of the furcae, each branch passing to the tip. The bulbous expansions which project beyond the furcal tips in *C. bombayensis* no. 19 are absent in *C. elvae* (Fig. 24). The main collecting tube in the latter is more nearly an arm of the excretory vesicle, and its lateral bending is more anterior; just before giving off the anterior and posterior collecting tubules there are two dilations, in each of which is found a ciliated area. The details of the excretory system in *C. ocellata* were not completely worked out by Ssinitzin; he noted seven pairs of flame cells and a small pear-shaped excretory vesicle. Unfortunately the flame cells were not shown in the figures to which he referred, and the text statement appears to have escaped the notice of Sewell, who assumed an excretory system similar to that of *Cercariae indicæ* XXV and XXXVI and established an "Ocellata" group to include the three forms.

The group must be set aside and other disposition made of the members. The excretory system in *C. gigantea* was not completely analyzed.

The principal mass of cells which in part represents the reproductive system of the adult is located posterior to the ventral sucker. A similar mass was shown in *C. ocellata*, *C. bombayensis* no. 19 and *C. gigantea*. It has not been possible to trace definitely other scattered germ cells in *C. elvae*.

The two snail hosts both died and disintegrated during the author's enforced absence from the laboratory, so that the description of the parthenitae of *C. elvae* is lacking. One of eight large specimens of *Lymnaea stagnalis* var. *appressa* collected in Hook Point Cove, Douglas Lake, Michigan, on July 8, 1921, was infected; the second host was in a collection of twenty-three snails of the same species and variety from Bessey Creek on August 4, 1921.

### CERCARIA WARDI MILLER 1923

[Figs. 29-37, 43-45, 50-54]

Host, *Planorbis trivolvis*

Locality, Urbana, Illinois (old stream bed and pool)

Occasion, three times in April, 1921

This cercaria is less like the members of the schistosome group than is *C. elvae*. The forms which it resembles most closely are *C. bombayensis* no. 13 and *C. indica* XXV. All three possess a unique posterior gland, which in *C. wardi* reacts in such a way as to make it probable that the contents are of a mucin nature (Mathews, 1920:323; Hawk, 1921:112); the other two have not been examined in this regard.

This larva is readily visible to the naked eye when swimming about in a small glass container; although quite transparent, the rapid vibration makes it seen even in somewhat turbid water. The general type of spasmodic, intermittent locomotion common to most of the furcocercous cercariae is found; however, *C. wardi* has not been observed to swim with the tail forward. While sinking through the water, the tail is usually bent around so that the animal has, with variation, the shape of a horse-shoe. When cercariae have freshly emerged from the snail, the touching of any surface is sufficient to initiate rapid darting movements. Sometimes they creep upon the bottom, attaching alternately the anterior organ and the ventral sucker; this method of locomotion is not frequently employed, although fairly rapid progress can be made. When cercariae are kept in a stender dish for some hours, the periods of quiescence upon the bottom become lengthened; in the great majority of cases the animal is curled about, varying from a wide horse-shoe to a form in which the anterior end of the



body lies upon some part of the tail. Often the furcae project upward; when they, or any part, are touched with a needle or by another swimming cercaria, rapid locomotion is resumed. This is effected by rapid vibration of the whole animal, especially of the tail; however, progress does not necessarily accompany vibration; there is a node at the origin of the furcae and another at the junction of body and tail, and when the anterior organ is attached there is a third node at this point.

Some simple experiments on viability were carried out. An infected snail was placed in a small stender dish containing water of the stream in which it had been found; after about twenty cercariae had emerged, the snail was successively placed in stender dishes filled with tap water and with distilled water, and each was covered with a ground glass top. Observations were made several times daily. At the end of nine hours all the cercariae in distilled water were dead, and fifty per cent were decauded. At the end of two days those in stream and in tap water appeared to be normal; dead animals were observed for the first time on the morning of the third day. Some were alive at the end of four days, although none lived much longer. It is quite evident that their viability is very low in distilled water, and it would seem that emerged cercariae may be kept equally well in stream or tap water. It is possible that under more favorable conditions the length of life of some individuals after emergence might be considerably greater than four days. In this connection it may be noted that the human schistosome larvae are generally said to survive about forty-eight hours after emergence.

Sizes under various conditions are: maximum extension of a living cercaria, body 467  $\mu$ , tail-stem 730  $\mu$ , entire tail 935  $\mu$ ; well-extended specimens which had been mounted in Canada balsam for two years (average), body 243  $\mu$  by 69  $\mu$ , tail-stem 564  $\mu$ , furca (to extreme tip of fin-fold) 202  $\mu$ ; unstained cercariae recently mounted in Canada balsam (average), body 265  $\mu$ , tail-stem 682  $\mu$  by 50  $\mu$ , furca 273  $\mu$ . Body width is not easily determined, due to the irregular outline presented; in occasional specimens which showed a dorsal view in the freshly mounted material the body averaged 75  $\mu$  wide. *C. wardi* is somewhat smaller than either *C. bombayensis* no. 13 or *C. indica* XXV, but in all three the proportions of body to tail-stem to furcal length are practically identical.

There is a prominent ventral sucker, located somewhat posterior to the middle of the body; it almost always protrudes decidedly, and therefore a lateral view is the one usually obtained under a cover glass. Its greatest diameter measures 28  $\mu$ ; when completely everted, it has a rounded cone-shape (Fig. 34), and a cap of small spines extends about 20  $\mu$  back from the tip. *C. bombayensis* no. 13, which Soparkar noted to be often seen lying on its side, and *C. indica* XXV also have prominent ventral suckers.

The entire surface of the animal is covered with fine spines, except that part of the anterior organ which is protrusible; this agrees with the description for *C. indica* XXV. Because of confusion in Soparkar's use of the word *tail*, just what the exact condition is in *C. bombayensis* no. 13 is not clear. In most of his descriptions he distinguishes between *tail* and *furcae*, or *furcal rami*; but in illustrations the parts of the tail are labelled *stem of tail* and *furcal rami*. Another example of the confusion is in the case of *C. bombayensis* no. 19, where the figure shows both tail-stem and furcae to be spined, and the description states that the body and *tail* are covered with spines; here *tail* is evidently meant to include both parts, although in the preceding sentence tail and furcae are used. In the drawing of *C. bombayensis* no. 13 the furcae are shown without spines; the statement is, "both the body and the tail are covered with spines and the furcal rami have a thin membrane attached to them." It is probable that spines are not present on the furcae, both because they are absent in the figure, and because tail has been usually used for tail-stem. The spines on the ventral sucker of *C. wardi* are larger than those on the cuticular surface; those on the anterior organ are small, retrorse, and very closely set together in diagonal rows, so as to give the appearance of the surface of a fine file.

The anterior organ is not distinctly divided into a thin-walled anterior and a muscular posterior part, although it is furnished with circular muscles in the latter region (Fig. 32). The head gland is median and dorsal (Fig. 43), and varies somewhat in size in different individuals; its exact nature has not been determined, but it is apparently more similar to that of *C. bombayensis* no. 13 than of *C. indica* XXV. In the latter two large refractile cells were noted, with clear nuclei, and apparently with ducts opening anteriorly; whether these cells are equivalent to the head gland in schistosome and nearly related larvae is a matter for further investigation.

The tail-stem is more than twice as long as the body; it is firmly attached, as decauded specimens are rarely met with. It has prominent muscles passing spirally around the proximal part, which straighten gradually until in the distal third they are parallel to the longitudinal axis. This condition exactly duplicates that found in *C. indica* XXV. The muscles are distributed in four fields (Fig. 45); there is a central area of large cells in the tail-stem which appear quite clear, and the caudal excretory tube passes through the center. The furcae are delimited from the tail-stem and are furnished with wide and thin dorso-ventral fin-folds (Fig. 51). What appear to be thickenings are seen at irregular intervals and are due to fluting (Fig. 44).

There is a large H-shaped nervous system lying behind the anterior organ and extending forward somewhat on each side of it; the compound eye-spots are posterior to it, about two-fifths of the body length from the anterior end. Each is composed of a number of large brown-black granules

arranged to form a cup, with the open side dorso-lateral (Fig. 52). In living cercariae they appear almost spherical,  $13\ \mu$  by  $15\ \mu$ , and lie in a clear area  $22\ \mu$  in diameter. No similar pigment was observed in any other part of the body. Soparkar did not describe the nervous system of *C. bombayensis* no. 13; the eye-spots in this form are composed of dark granules, and there is a refractile lens in the center of the mass. *C. indica* XXV has an irregular mass of nervous tissue anterior to the salivary gland cells and dorsal to their ducts; the eye-spots are in contiguity with its anterior surface, in contrast to their posterior location in *C. wardi*. That the latter condition is more usual is supported by the statement of Faust (1918), "the eye-spots of the binocular species are usually in direct connection with the posterior dorsal nerve trunks." However, in *C. gigas* (Faust, 1918b) and in *C. douthitti* (Cort, 1915) they are connected with the anterior rami.

The mouth is a small opening on the ventral surface of the anterior organ, about  $22\ \mu$  from the tip; the esophagus passes through the anterior organ close to the ventral wall, and penetrates the posterior wall. From this point the esophagus passes ventral to the eye-spots, enlarges, and bifurcates into large ceca, the length of which varies somewhat in different individuals. There is no trace of a pharynx.

At least three different kinds of glands are present; the ordinary type of penetration glands encountered in the schistosomes and nearly related larvae will be considered first, after which the posterior mucin gland, so far reported for only the three larvae discussed here, will be described. There are two sets of penetration gland cells, an anterior group of four, and a posterior group of six. It is clearly seen in the living animal, as well as in sections, that the protoplasm of the anterior cells is coarsely granular, while that of the posterior is very fine (Fig. 50). The distinction is further seen in the staining reactions; the former group is eosinophilic, and the latter basophilic to Delafield's hematoxylin; when hematoxylin is used alone, the anterior cells are chromophobic. In general, then, these two sets of glands are similar to those in certain of the schistosomes and allied forms. Faust (1921d) stated that "a comparative study of the effects of these glands on host tissues indicates that basophilic and acidophilic glands are complementary in function and that a larva possessing the two differentiated types can penetrate the host much more effectively than one possessing one type. The schistosome cercariae are notable examples of the dimorphic type of staining reaction." This last sentence seems to the author to be unjustified, in view of the fact that of the five cercariae known to be the larvae of schistosomes, namely those of *Schistosoma japonicum*, *S. haematobium*, *S. mansoni*, and *S. spindale* and *Schistosomatium pathlocopticum*, only the first three were described at the time of Faust's writing;

and of these only the larva of *S. mansoni* had been reported to have two sets of glands (Faust, 1920a). The larva of *S. spindale* (Soparkar, 1921) was subsequently described as having an anterior group of four eosinophilic cells, coarsely granular, and a posterior set of six with slightly larger nuclei and finely granular or almost homogeneous protoplasm; with intra-vitam staining the anterior cells remain unstained and the posterior stain deeply. This reaction was not studied in *C. wardi* or *C. elvae*. The ducts from the two groups of gland cells pass ventral to the alimentary canal, eye-spots, and nervous system (Fig. 52), and enter the anterior organ ventro-laterally just at the junction of its two regions. They then continue through the substance of this organ and open at the anterior tip, probably through spines which cap the duct openings; these are seen only with difficulty in stained specimens.

The posterior mucin gland is of particular interest (Figs. 36, 37). What are probably homologous structures have been reported for *C. indica* XXV and for *C. bombayensis* no. 13. For the former Sewell stated: "Behind these cells is a large and somewhat horse-shoe shaped mass of finely-granular protoplasm in which I was unable to detect any cell outlines, nor could I see any corresponding ducts, but I take it to be the posterior part of the salivary gland." Soparkar described, behind the rudimentary genital system, "a large irregular cell with coarse granules which takes a deep stain when colored by the intra-vitam method. It is difficult to say what function this large gland-like structure performs. No duct arising from it could be made out." In living *C. wardi*, mounted in water and examined by transmitted light, this posterior mass is clearly defined, and seen to be homogeneously granular and somewhat yellow. Definite ducts leading anteriorly from it can not be clearly observed, although up to the region of the eye-spots, where they seem to converge, and less clearly between them, some of this same yellowish granular material is seen. In well-cleared specimens it was possible to trace these granules farther to the anterior than Sewell found them in *C. indica* XXV. Study of sections of immature forms revealed the fact that this posterior mucin gland is composed of many small cells, although the cell outlines are not seen in mature larvae and only an occasional nucleus is observed. In an attempt to determine the nature of this structure some specimens were killed in warm saturated aqueous solution of corrosive sublimate, and after washing for a few hours in distilled water were stained with dilute thionin in one percent phenol. From the fact that this posterior granular gland and the lateral extensions from it stain reddish, while the surrounding tissue is blue, would seem to indicate that this is a typical meta-chromatic reaction, and that the contents of the gland are of a mucin nature (see Lee's Vade Mecum, 1921:133, 391). Simple aqueous solutions of both thionin and toluidin blue were also employed, following the method of LaRue (1915), with equally good results.

There are five pairs of flame cells in the body (Figs. 30, 31), and except for minor details of relative position and length of capillaries the excretory system is identical with that of *C. bombayensis* no. 13; the distal part of the main excretory tube on each side is provided with two ciliated areas. *C. indica* XXV has four pairs of flame cells in the body and no cilia were noted in the excretory tubes. The island of Cort is apparently absent in all three; each has one pair of flame cells in the tail-stem. *C. indica* XXV is quite different also in that the caudal excretory tube is distended to equal one-third of the tail-stem diameter throughout the greater part of its length. In all three, branches pass through the furcae to open at the tips, without bulbous extensions.

A single prominent mass of germ cells is present in each larva, similarly situated and probably representing the same organ of the adult. In spite of Sewell's statement that "the genital organ is represented by a compact mass of small round cells situated ventrally, immediately behind the acetabulum and between the paired salivary-gland cells and the undifferentiated cell mass noted above," it is clear, from a comparison of his figures referred to, that the genital mass appears to be close to the ventral sucker only when seen from the ventral side. This is also the case in *C. wardi*, the lateral view of which clearly shows that the mass of germ cells really lies almost mid-way from the ventral sucker to the posterior end of the body. The apparent inconsistencies are seen to be due in both cases to the body shape of the larva and the positions typically assumed in consequence. Although Sewell assumed that this germ cell mass represented the future ovary of the adult, the author believes that until more is known concerning the development of the reproductive system, and sexual dimorphism in cercariae, the definite naming of the larval fundaments is hazardous.

The liver tissues of the infected snail are found to be filled with masses of sporocysts of varying length and caliber, so tangled that it is difficult to dissect them unbroken. They are very irregularly constricted; the diameter never exceeds 100  $\mu$  and is about 15  $\mu$  at points of greatest constriction; the longest one dissected free measured 1.4 mm. The cercariae develop in bunches at irregular intervals within the sporocyst (Fig. 53), at the regions of greatest diameter; these are much more transparent than the constricted portions of the tube. Throughout the length are found occasional granules of orange-yellow pigment, and the more opaque narrow regions contain sufficient numbers of minute pigment granules to produce a pale yellow color. Upon all three occasions on which *C. wardi* was found the host was *Planorbis trivolvis*, from a restricted region just north of Urbana, Illinois. On April 6, 1921, thirteen large individuals were collected in a pool northeast of the cemetery; of these one harbored the parasite. From an old stream-bed in Colvin's Field one in thirty-seven, collected April 7, 1921, was found to be infected. Another parasitized snail in a total of twenty-

nine was collected April 19, 1921, from a point farther north in the same stream-bed. In the first and last collections the infections with *C. wardi* were the only ones found; in the second, two other individuals were parasitized with immature furcocercous forms, the identification of which was impossible.

#### PHARYNGEAL LONGIFURCATE DISTOME CERCARIAE

#### CERCARIAE BURTI MILLER 1923

[Figs. 46-49, 55-58, 62-66]

Host, *Planorbis trivolvis*

Locality, Burt Lake, Michigan (Colonial Point)

Occasion, once in August, 1921.

This cercaria is similar to *C. douglasi* (Cort, 1917:53) which was found in *Physa ancillaria* in the same region. Dr. Cort kindly loaned several slides of this larva. The two are alike and unique in certain features of the excretory system. The general appearance of a number of swimming *C. burti* is similar to that of any other furcocercous form with long furcal rami; locomotion is usually upward, with tail in advance. Under a cover glass there is less activity than is usually seen, and the body is for the most part held contracted into an oval shape. With the ventral sucker attached to the substratum, vibrations of the tail may cause slight rotation on it as a pivot, but never complete turning about. Great changes in body length are possible; the extended body is a blunt-ended cylinder longer than the tail-stem, which is much less contractile.

In permanently mounted material all degrees of contraction and extension are seen; for purposes of determining size, individuals which were moderately extended were chosen, and these give the following measurements (average): body 134  $\mu$  by 35  $\mu$ , tail-stem 140  $\mu$  by 26  $\mu$ , furca 157  $\mu$ . The tail is often distorted, so freshly-made mounts in Canada balsam were measured, and here the diameter of the tail-stem equals or exceeds that of the body; maximum sizes are: body 157  $\mu$  by 34  $\mu$ , tail-stem 142  $\mu$ , furca 157  $\mu$ ; minima: body 88  $\mu$  by 52  $\mu$ , tail-stem 113  $\mu$ , furca 139  $\mu$ . In the living animal under a cover glass the length of the body at extreme extension is 240  $\mu$ , while the usual size is, body 125  $\mu$ , tail-stem 165  $\mu$ , furca 181  $\mu$ . The sizes given for *C. douglasi* are, body 150  $\mu$ , tail-stem 180  $\mu$ , furca 160  $\mu$ . These were presumably made from mounted material; the author has made measurements from type material of this form which practically coincide with Cort's, and which give a body width of 35  $\mu$  when the length is 157  $\mu$ . The two cercariae agree in that the body, except in extreme extension in *C. burti*, is shorter than the tail-stem; in *C. douglasi* the furcae are shorter than the tail-stem, while in *C. burti* they are consistently longer.

The anterior organ is short, not infrequently almost spherical, or it may be pyriform with either the small or the large end to the anterior. It is not divided into an anterior and a posterior region, nor is there the external constriction which usually accompanies that condition. The entire organ is a thin-walled sac, apparently not muscular. Its length in both cercariae averages 30  $\mu$ . There is no trace of a head gland in either. The ventral sucker, situated posterior to the mid-point of the body, is a strong organ of attachment. It extends up into the body and never protrudes prominently, so that a frontal view is the usual one obtained; often it is completely retracted into the body (Figs. 46, 49). Its circular edge is furnished with several rows of small spines, easily visible, which doubtless aid in attaching the organ to a substratum. In mounted material the greatest diameter of the ventral sucker of *C. burti* is about 25  $\mu$ , while in *C. douglasi* the average of a number of measurements is 21  $\mu$ .

The body and tail spination agrees in general with the brief statement for *C. douglasi*. The anterior organ region is covered with blunt, rather large spines which become more sparse in the region immediately posterior to it and are absent from the rest of the body surface. The tail-stem and furcae are only very sparsely spined. The tail-stem is attached strictly posterior to the body, and the union is evidently a strong one, as decaudation takes place very late when the animal is subjected to increasing pressure under a cover glass. There is a definite annulation of the wall, no doubt due to the contraction of circular muscles lying just under the cuticula. In the living animal the presence of caudal glands and their ducts is readily detected (Fig. 66); they are also seen in many mounted specimens. They are variable in number and arrangement, although the four anterior pairs are usually symmetrically arranged around the central excretory tube. Toward the posterior they may be very irregular in number, shape and location; in some individuals there are eight symmetrical pairs, while in others only a few small pear-shaped cells, irregular as to size and position, are seen in the entire length; this lack of regularity is similar to that recorded for *C. multicellulata*. The tail-stem has exceptionally weak musculature; while there are four muscle fields (Fig. 59), each is apparently composed of a single fiber, which does not stand out conspicuously from the wall. The furcae are laterally flattened, and when not under pressure are held so that their thin edge is seen when looking at a dorsal view of the larva; upon increase of pressure they are turned so that the broad side is seen, which shows a sword-like shape slightly narrowed proximally. As is common with longifurcate forms, there is no constriction between furcae and tail-stem.

The central nerve cell mass is H-shaped, posterior to the pharynx, with the anterior branches lateral to, and extending forward beyond it. No

pigmented eye-spots are present, nor any cells which might represent unpigmented eyes. The system in *C. douglasi* presents no striking differences.

The opening of the alimentary canal is terminal; the narrow esophagus passes through the anterior organ (Fig. 55), pierces its posterior wall, and continues as a short prepharynx. The pharynx is readily seen in both living and mounted specimens; in the former its diameter is  $13\ \mu$  and in the latter  $9\ \mu$ . Posterior to the pharynx the esophagus continues to the ventral sucker, where it bifurcates into narrow ceca. These are ventral to the penetration gland ducts (Fig. 49) and terminate just in front of the penetration gland cells; the distal part of each is contiguous posteriorly with two disjointed parts (Fig. 65). This condition is doubtless comparable to that which Sewell described for *C. indica* XXII. The ceca are described for *C. douglasi* as extending two-thirds of the distance between the acetabulum and the posterior end of the body. In *C. burti* the walls are relatively thick and are chromophobic to hematoxylin and the eosins; the contents are a granular mass which fills the lumen and stains very deeply with eosin.

In the living animal the penetration gland cells and ducts are seen only with great difficulty, even with high magnification and with oil between the condenser and object slide. The cells are confined to the postero-dorsal part of the body; there are eight of them, containing granular cytoplasm which is eosinophilic and vesicular nuclei which scarcely stain except for a prominent acidophilic plasmosome (Fig. 60). Whether the coarsely granular nature of the cytoplasm is due to fixation is not known, as observations on living cercariae were unsatisfactory because of the presence of many small parenchyme cells. One observation on the ducts of a living animal showed them passing the pharynx laterally, curving to the middle of the body, and entering the anterior organ at its posterior end; in mounted material they seem to enter postero-laterally. *C. douglasi* has four penetration glands.

The excretory system indicates close relationship to *C. douglasi*; the total number of flame cells is the same in each, but their distribution is different. The feature in which the two cercariae are unique is in the presence, anterior to the ventral sucker in *C. douglasi* and posterior to it in *C. burti*, of a cross-commissure connecting the two main lateral collecting tubes (Fig. 63). The excretory vesicle lies just anterior to the junction of the tail and is small and oval; its long axis is perpendicular to the body length and measures about  $12\ \mu$  in the living animal. Less frequently it is seen as a crescent, when the lateral arms are swollen. While Cort's diagrammatic representation was probably not intended to show excretory vesicle shape, his figure indicates a somewhat different form for that structure in *C. douglasi*. An island of Cort is present in both larvae. There is a tangled mass of the main lateral collecting tube at either end of the cross-commissure, which finally gives rise to anterior and posterior collecting



tubules. The former drains flame cells I and II, which lie anterior to the ventral sucker; the latter subdivides into three tubules at a point about two-thirds of the distance from the ventral sucker to the posterior end of the body. One of these fine tubules drains flame cells III and IV, which are located in and lateral to the complex convolutions; another drains flame cells V and VI in the posterior region of the body; the third comes from the single flame cell in the proximal part of the tail. In comparison, there is an anterior set of three flame cells and a posterior set of two on each side of the body of *C. douglasi*; there are two pairs in the proximal region of the tail, in contrast to the single pair in *C. burti*. Until there are more data on the development of the excretory system from the arrangement found in the cercaria, the closeness of relationship of two such forms cannot be predicted. In both larvae the caudal excretory tube passes through the tail-stem, is attached to the distal end just between the furcae, and divides to continue down one half the length of each ramus to open by a simple pore to the exterior.

The genital system is represented by an irregular mass of small chromophilic cells (Fig. 64) located in the posterior part of the body, just behind and extending slightly forward between the penetration gland cells. Similar scattered cells are found to the anterior, but there are no definite aggregations.

The parthenitae are long thin-walled sporocysts, very much tangled in the liver mass and difficult to dissect entire. The longest piece freed measured more than five millimeters in length, with a range of from 46  $\mu$  to 184  $\mu$  in diameter (Fig. 47). The cercariae develop in batches, between which the sporocyst is constricted and the walls may be quite thick; the lumen is continuous. Very frequently a large number of larvae, in all stages of development, are present in the same dilated portion. A birth-pore is present near the anterior end (Fig. 48). Cort did not describe the parthenitae of *C. douglasi*; the largest piece found on one of his slides was 1.3 millimeters long and 0.19 millimeters in diameter. It resembled very closely those just described; no unbroken ends were found and therefore it is not known whether a birth-pore is present.

This larva was found once, from a collection of *Planorbis trivolvis* taken in a swamp near Colonial Point, Burt Lake, Michigan on August 9, 1921. Seven out of seventy-three individuals were parasitized with *C. burti*; three other infections with furcocercous cercariae were found, beside two with echinostome and two with stylet cercariae, in the same collection.

## CERCARIA TENUIS MILLER 1923

[Figs. 59-61, 67-77]

Host, *Planorbis trivolvis*

Locality, Burt Lake, Michigan (Colonial Point)

Occasion, once in August, 1921.

This is a very slender-bodied pharyngeal larva. It is an interesting fact that it is strikingly similar to an Indian representative of the small group of apharyngeal longifurcate distomes, and not to any of the numerous pharyngeal forms. *C. gladii* Cawston 1918 (according to Faust 1919a: 164) and *C. indica* XXII Sewell are the only two carefully studied longifurcate cercariae which lack any trace of a pharynx, and it is to the latter form that *C. tenuis* is similar in many respects.

There is nothing unique in the locomotion of *C. tenuis*; under a cover glass it progresses by taking hold alternately with anterior organ and ventral sucker, while the tail is rather passive; usually both tail-stem and furcae do not appreciably change their shape or length, but are held straight, with the furcae almost touching or each bent to the side. The sides of the body are usually parallel, with the posterior end square, and the anterior end bluntly rounded. There are no marked changes in body form except those of contraction and extension. The sizes under various conditions are: mounted in Canada balsam, well-extended (average), body 225  $\mu$  by 21  $\mu$ , tail-stem 216  $\mu$  by 21  $\mu$ , furca 207  $\mu$ ; maximum extension of living animal, body 288  $\mu$ , tail-stem 240  $\mu$ , furca 240  $\mu$ .

The anterior organ is oval, or sometimes pyriform with the small end posterior; its average length in mounted material is 45  $\mu$ . The wall is thin and non-muscular, not differentiated into anterior and posterior regions. The ventral sucker (Fig. 67) is about three-fourths of the body length from the anterior end, and averages 25  $\mu$  in diameter. There is a single row of twenty-two hooked spines (Fig. 71) around its edge; the spines are attached with the hook projecting and pointing toward the center, so that when the sucker takes hold of a substratum, they aid in attachment. On the body surface of *C. tenuis* there is an oral cap of spines which are rather small and sparsely distributed; a slight gradation is exhibited, from large in front to smaller toward the posterior limit of the spined area. The spines are like those of *C. chrysenterica*; the portion from *a* to *c* is embedded (Fig. 80), and *b* projects, pointing toward the posterior. The remainder of the body and the tail is not spined.

The tail is attached terminally to the body, and in the living cercaria it is more narrow; in well-extended specimens mounted in Canada balsam the two diameters are about equal. Fine annulations are present throughout the entire length, and the cuticula is very thin; there are neither spines

nor sensory hairs. About five pairs of caudal glands are present, which do not differ from those found in *C. burti*; number, form, and arrangement are not constant. The usual slender outgrowths, which lead to the wall of the tail-stem and evidently may act as ducts, are present. The furcae are broadly lanceolate and terminate in sharp points, and are not delimited from the tail-stem. They are much more transparent than either body or tail-stem.

The nervous system is represented by an irregular H-shaped mass located in the anterior part of the body, generally behind the pharynx; the anterior branches extend lateral to this organ. Eye-spots are lacking. The mouth is subterminal, and the esophagus (Fig. 70) leads back to pierce the posterior wall of the anterior organ. The prepharynx is  $8\ \mu$  long; the pharynx is clearly outlined and its greatest diameter is  $11\ \mu$  in living cercariae,  $8\ \mu$  in mounted material. Just behind this the esophagus is dilated; it bifurcates into long ceca not quite midway of the body, and these pass around the ventral sucker to end in two disjoined but contiguous parts (Fig. 75). These, as in *C. burti*, may be interpreted as sections which have not yet broken through to form a continuous lumen. The esophagus shows regular cross striations. The wider ceca, dorsal to the penetration glands (Fig. 76), contain a homogeneous mass which is eosinophilic in sectioned material.

The penetration glands are located in the region just anterior to the ventral sucker; the details of all structures in this area are obscured by numerous parenchyme cells. In the living animal the penetration glands show as a coarsely granular, grayish and ill-defined area; in a few specimens it is possible to see four definite cells, with rather large refractile nuclei. The confirmation of this comes from the study of sections, in which the number of the glands and their position with reference to the alimentary canal may be determined. The cytoplasm of these cells is chromophobic to Delafield's hematoxylin in toto and in sections, and eosinophilic in sections. The ducts frequently appear empty, but when the contents are present they also are eosinophilic. They are difficult to trace except in sections (Fig. 70). In the region of the openings of the ducts there are about eight prominent spines; they are probably arranged in a semi-circle around the dorsal side of the mouth opening. *Cercaria indica* XXII was said to be crowned with anteriorly-directed spines.

The presence of five pairs of flame cells in the body, in about the positions given them (Fig. 74), can be affirmed, as well as two pairs in the tail-stem. The exact connections of the capillaries with the collecting tubules and of these with the main lateral collecting tubes, are not known beyond all possible question; the arrangement shown is the probable one. The excretory vesicle is a tripartite structure composed of a central vesicle and two large dilations of the proximal ends of the main lateral collecting tubes.

An island of Cort is probably present in *C. tenuis*. The caudal excretory tube passes through the center of the tail-stem and the four flame cells are very close to it; after it bifurcates each branch passes through half the length of the furca, to open to the exterior by a simple pore on the edge.

The genital system is represented by a mass of cells in the posterior part of the body, not so close to the junction of body and tail as in those larvae in which the penetration gland cells are crowded behind the ventral sucker. *C. tenuis* develops in long sporocysts, which do not exhibit the variations in diameter shown by those of *C. wardi* or *C. burti*; the lumen is more evident through the entire length, and the cercariae are not so definitely separated in batches (Figs. 72, 73). The cuticula of the sporocysts, like that of the larva, is very thin. A birth-pore is located near one end, and the opening is in a marked prominence on the surface; the canal through the thick wall is not always seen in total mounts, but the raised lips locate the opening.

Two out of seventy-three specimens of *Planorbis trivolvis* collected in the Colonial Point Swamp, Burt Lake, Michigan, on August 9, 1921 were parasitized with this larva; it was in the same collection with *C. burti*.

### CERCARIA CHRYSENTERICA MILLER 1923

[Figs. 78-94]

Host, *Lymnaea megasoma*

Location, Burt Lake, Michigan (Colonial Point)

Occasion, once in August, 1921

This is the first larval trematode to be reported from *Lymnaea megasoma*, which has a restricted distribution in the north central United States and extends far up into Canada (Baker, 1911). *C. chrysenterica* is a longi-furcate form, and is quite similar to *C. emarginatae* (Cort, 1917:53); the author received slides of this species through the kindness of Dr. Cort. *C. letifera* (Fuhrmann, 1916:389) will be included in the same group because of general likeness, but descriptions of the penetration glands and of the details of the excretory system are lacking. All three larvae have very long intestinal ceca, which in the first two are dilated distally and filled with a yellow jelly-like substance.

The method of locomotion is not unusual; the body is pulled after the tail in short straight dashes, or longer erratic ones, generally upward through the water. Under a cover glass there may be some progress with the body in advance, for short distances only; the tail lashes actively. The cercaria may move slowly by alternate use of anterior organ and ventral sucker, with accompanying form changes (Figs. 92-94).

Sizes under various conditions are: well-extended specimens mounted in Canada balsam (average), body 260  $\mu$  by 48  $\mu$ , tail-stem 244  $\mu$ , furca

248  $\mu$ ; maximum body extension of living cercaria, 384  $\mu$ . These measurements are slightly larger than those given for *C. letifera*, which is in turn larger than *C. emarginatae*; however, the author's measurement of a large individual of this latter species on one of Cort's slides gave body 254  $\mu$  by 37  $\mu$ , as against a body length of 160  $\mu$  given by Cort.

The body of the living animal is the shape of a spindle with the greatest diameter just behind the ventral sucker, and a gradual tapering from this point to the anterior. The anterior organ is usually pyriform, with the small end posterior, although it may be oval. There are not two regions as distinctly differentiated as in *C. elvae*, although the posterior part is more strongly muscular than the anterior; there are both longitudinal and circular fibers (Fig. 90). In *C. letifera* and in *C. emarginatae* the anterior organ is of the same general shape as that just described. No one of the three cercariae has a head gland. The ventral sucker is about two-thirds of the body length from the anterior end, but its relative position varies with the state of contraction. It is relatively large, especially in comparison with its size in the schistosome cercariae; in living larvae under some pressure of cover glass it is about 45  $\mu$  in diameter, while in permanent mounts it shrinks to 31  $\mu$ . It does not protrude markedly from the body (Fig. 89). There are small spines around its edge. In *C. letifera* it is smaller, and likewise it is spined; in *C. emarginatae* its diameter is 25  $\mu$  in mounted specimens.

There is an oral cap of spines like those described for *C. tenuis*. Behind these there is a small area on which small straight spines are present; this is followed by a short region with no spines. Between this bare region and the ventral sucker are eight or nine irregular bands, each composed of two or three rows of spines. The region around and posterior to the ventral sucker is uniformly covered with spines. For *C. emarginatae* the statement is made, "heaviest spination around acetabulum, with rest of body only sparsely covered." Fuhrmann reported only four or five large spines on the anterior extremity of *C. letifera*.

The tail is attached terminally to the body and is quite transparent; the surface of the tail-stem is finely annulated. The number of caudal glands varies in different individuals, from four to eight or more pairs. They are relatively small and do not take up a great part of the tail-stem cavity (Fig. 78); the usual ducts lead to the outer surface. The furcae are broad and flattened.

The nervous system is represented by an H-shaped mass which extends somewhat to the anterior on each side of the pharynx. This system is not reported for *C. letifera* or for *C. emarginatae*. There are no eye-spots.

The mouth opening is subterminal; the esophagus passes through the anterior organ and penetrates its posterior wall. The prepharynx dilates just in front of the pharynx, and the latter is about 20  $\mu$  in diameter in the living animal, shrinking to 15  $\mu$  after preservation. The esophagus con-

tinues to about midway of the body, passing ventral to the nervous system (Fig. 84), and then bifurcates into ceca which approach the dorsal wall and gradually increase in diameter (Figs. 86, 89). The walls of the ceca are thick, and several nuclei are present in them; the contents within the lumen appear jelly-like and homogeneous, and stain deeply with eosin. From a study of Cort's material of *C. emarginatae*, the author finds an alimentary canal quite similar to the one just described. It is difficult to compare it to that of *C. letifera*, as Fuhrmann's account is incomplete and it is not clear as to the location of the pharynx.

The penetration gland cells are confined to the region median and posterior to the ventral sucker; they are four in number and are readily seen in the living animal. One cell on either side is lateral and ventral to the cecum; the remaining two are median, in tandem position, and so laterally compressed as to be almost in contact with dorsal and ventral body walls (Fig. 86). In a living cercaria the protoplasm of all four cells is coarsely granular; after fixation there is no definite staining reaction to either Delafield's hematoxylin or to eosin, and the greater part of the contents seems dissolved out. The ducts of the lateral cells pass forward ventral to the ceca, and those of the median cells may be contiguous for a little way (Fig. 89). The two of each side come into contact at about the level of esophageal bifurcation, and pass forward together, bending medially to enter the anterior organ. In connection with the duct openings, there are about twenty-two solid piercing spines, arranged in a semicircle around the dorsal edge of the mouth opening; the ten median spines are somewhat larger than the others. In comparison, Cort's account for *C. emarginatae* stated that there were six glands, extending into the post-acetabular region; the author's examination of Cort's material shows the cytoplasm to be coarsely granular and chromophobic to Delafield's hematoxylin in total mounts. Fuhrmann did not include the penetration glands in his description of *C. letifera*.

There are nine pairs of flame cells, three anterior to the ventral sucker, four in the posterior region, and two in the tail-stem (Fig. 79). *C. emarginatae* has the same number anterior to the ventral sucker, but they form one group on each side, with their capillaries emptying into the larger tubule at one point; in *C. chrysenterica* flame cells I and II have apparently arisen from the division of a cell, and are not near III, whose capillary joins separately. Posterior to the ventral sucker *C. emarginatae* has but two pairs of flame cells, the capillaries of which join the posterior collecting tubule at the same point; it has two pairs in the tail-stem, more distally located than in *C. chrysenterica*. Fuhrmann figured none of the excretory system of *C. letifera* except the excretory vesicle outline, so it cannot be included in the comparison.

The genital system is chiefly represented by a somewhat wedge-shaped mass of cells located in the posterior end of the body, just in front of the excretory vesicle and between the ends of the ceca. Anterior to the ventral sucker and extending up toward the origin of the ceca there are two masses of cells which correspond in position to the vagina and cirrus pouch shown by Faust for *C. gracillima* (1918). The relation of these cell groups to the large posterior mass in *C. chrysenterica* is not clear.

The parthenitae are long tubes of varying diameter, which exhibit gradual swellings in several regions, and so are unlike other sporocysts described which have ball-like swellings. The longest entire individual dissected free from host tissue measured more than 8 mm. in length, and was 180  $\mu$  and 60  $\mu$  in greatest and smallest diameters; in one preparation of sections a maximum diameter of 244  $\mu$  was observed. The walls of the narrow regions are thicker, although a prominent lumen extends throughout. The anterior end is distinguished by a solid knob of small cells, behind which the prominent lips of the birth-pore are seen on one side (Fig. 83). Some sporocysts on Cort's slides were studied; they are quite similar to those just described, both in the caliber of the tube and in the presence of a definite birth-pore with prominent lips. Fuhrmann described the sporocysts of *C. letifera* and figured an individual containing immature larvae; a birth-pore was not observed.

*C. chrysenterica* was found once only, in a collection of *Lymnaea megasoma* from a swamp near Colonial Point, Burt Lake, Michigan on August 9, 1921. One snail out of eighteen was parasitized.

#### PHARYNGEAL LONGIFURCATE MONOSTOME CERCARIAE

#### CERCARIAE MULTICELLULATA MILLER 1923

[Figs. 1-8, 17, 18]

Host, *Physa gyrina*

Locality, Urbana, Illinois (Drainage Ditch)

Occasion, twice, in September and November, 1922

*Cercaria multicellulata* is the second pharyngeal monostome larva with long furcal rami to be described, the first being *C. rhabdocaeca* Faust (1919c: 338); its similarities to this cercaria and to *C. hamata* Miller will be considered in the discussion of the latter elsewhere in this paper. No trace of an alimentary canal has been observed in this larva, but because of its striking similarities to *C. rhabdocaeca* and *C. hamata* the presence of a pharynx, obscured by the small parenchyme cells, is assumed. Another reason for including *C. multicellulata* with the pharyngeal forms is the number of differences between these three larvae and the only apharyngeal

longifurcate monostome, *C. indica* XXVII, especially with regard to the excretory system.

*C. multicellulata* swims sporadically; rapid dashes, generally upward, are effected by lashing of the tail, which is in advance. Between dashes the cercaria sinks body first, the tail-stem is extended in a straight line with the body, and the furcae are spread at an angle of about  $100^{\circ}$ . It is positively phototactic. A series of movements, probably connected with the entrance of the cercaria into a host, is frequently observed under a cover-glass (Text-fig. 2). From a condition in which the body is somewhat contracted and the anterior end turned in (A), the generally rounded contour of the anterior organ is changed to a pyriform shape as it is slowly extended a little (B). The anterior part of the body is then quickly thrust forward; the fore part of the anterior organ rapidly everts and presents the large, anteriorly-directed spines (C). The whole is then quickly retracted, rounded up, and the anterior-most part in (A). This series of movements is frequently alternated with one in which the everted part of the anterior

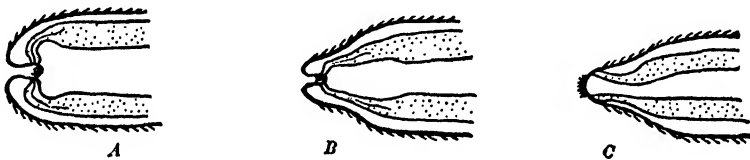


Fig. 2

organ (C) is rapidly thrust forward again and again, without rolling in and rounding up when withdrawn. The anterior organ has an attaching function also; it is strong enough to hold the cercaria to the under surface of a cover glass which is being pushed along a slide.

Sizes under various conditions are: maximum body extension under cover glass but free-moving,  $184\ \mu$ ; almost immobile from neutral red (average), body  $170\ \mu$  by  $37\ \mu$ , tail-stem  $230\ \mu$ , furca  $225\ \mu$ ; fixed in hot Gilson's fluid (average), body  $156\ \mu$  by  $28\ \mu$ , tail-stem  $198\ \mu$ , furca  $147\ \mu$ ; well-extended specimens mounted in Canada balsam (average), body  $136\ \mu$  by  $26\ \mu$ , tail-stem  $196\ \mu$  by  $24\ \mu$ , furca  $147\ \mu$ .

When under no compression the sides of the body are parallel up to the region of the anterior organ, where they taper off to a blunt end. With great extension the whole body tapers slightly from the posterior, and the anterior two-thirds may be crenated in the region behind the anterior organ; this crenation is due to the contraction of circular muscles just beneath the surface. The anterior organ varies from an oval to a pyriform shape in changing from a position of rest to extension; infrequently it contracts in the middle, becoming dumb-bell shape. It is approximately one-fourth as long as the body, although this proportion varies, since the anterior half of the body undergoes more extension and contraction than



the posterior. The anterior organ is armed with large retrorse spines extending over somewhat less than the anterior half, behind which they are both smaller and more sparse, so that, with the difficulty of observation due to the many small parenchyme cells in the body proper, it cannot be said whether they extend over the entire body; there is indication of sparse spination in somewhat definite bands back to the level of flame cell II. It may be noted here that the parenchyme cells, which are refractile, make difficult all observations on external and internal structure. The anteriorly-directed spines associated with the openings of the penetration gland ducts will be described in connection with those organs. The spination of *C. multicellulata* is on the whole very similar to that of *C. indica* XXVII, except that, in the latter, spines are reported for the anterior end and are shown as extending over only half of the anterior organ.

The cylindrical tail-stem is of less diameter than the body; the attachment is strictly posterior. Annulations, much finer than those of the body, are always noted; as Sewell suggests, these are due to the contraction of circular muscles directly beneath the delicate cuticula. The cells composing the wall have relatively large nuclei (Fig. 5) which quickly take a deep neutral red stain from dilute solution. Within the cavity of the tail-stem are ten to fifteen large gland cells, slightly yellowish in color and showing no granulation even under high magnification (1380 $\times$ ); they are arranged in pairs in the proximal portion, the caudal excretory tube passing between them, but farther to the posterior the pairing and size of the glands become irregular and they may lie on but one side of the excretory tube. While alive, the nuclei of these cells are seen to be relatively small and granular. Ducts lead to the wall of the tail-stem, and apparently open between surface cells. With contraction of the tail, the glands move within the lumen and the most posterior may be forced into one of the furcae. There is great diversity among different mature cercariae from the same snail; in some the glands are very clearly seen, while in others the outlines are so irregular that they can scarcely be recognized. As noted by Cort (1915) for *C. douthitti*, they are seen only in living specimens. While not clearly observable as such in the tail-stem of a living cercaria, four principal muscle bands (Fig. 6), strongly acidophilic, are seen in sections stained with Delafield's hematoxylin and eosin. On the surface there are delicate sensory hairs, seen only under high magnification and with proper lighting; their length is about three-fourths of the tail-stem diameter. No relation was observed between them and the openings of the caudal gland ducts. This is the second record of sensory hairs on the tail-stem of a furcocercous cercaria; they were previously reported for the distome, *C. letifera* Fuhrmann (1916). The furcae of a living cercaria are about equal in length to the tail-stem, and are not constricted at the base; they contract more than the tail-stem during fixation, and therefore appear shorter in permanent

mounts. There is an irregular lumen. On the surface are small spines in longitudinal rows, and the distal half is furnished with a narrow fin-fold which does not extend around the tip of the furca, nor is it thrown into folds such as are so characteristic of a form like *C. gigas*.

About three-fifths of the length of the body from the anterior end is located a pair of simple eye-spots, composed of from four to thirty black pigment granules of varying shape and size. The diameter of a group of granules composing an eye-spot is about 6  $\mu$ , and they are frequently observed, under a magnification of 1380 $\times$ , to lie in an irregularly-shaped clear area.

Repeated attempts were made to determine whether an alimentary canal is present. Only once or twice was some indication seen of a very narrow tube extending behind the anterior organ to a distance of about one-half its length; the observations were not conclusive.

There are three pairs of penetration gland cells (Figs. 5, 7). The anterior two are separated from the other four by a compact mass of cells, and their ducts are ventral to the others; all six pass dorsal to the eye-spots (Fig. 17) before dipping ventrally in the anterior half of the body; they become small before entering the anterior organ, and expand in that organ. The glands are more easily seen by intra-vitam staining with dilute neutral red; they take a deep red stain, while their ducts do not stain very deeply and are more yellowish, indicating either that they are empty or that the character of the secretion changes after entering them. That such a change from cell to duct may occur has been suggested by Faust (1920a); both cells and ducts appear coarsely granular. The entire penetration gland system is chromophobic to Delafield's hematoxylin in cercariae mounted in toto, but it is strongly eosinophilic when sections are counterstained with eosin. Between the openings of the ducts of the two sides there is a group of about twelve solid piercing spines.

The numerous parenchyme cells in the body make it especially difficult to determine the locations of flame cells and the connections of their ducts. The exact connections of all the small tubules could not be seen, but other details were made out (Fig. 5). The excretory vesicle proper consists of two parts about equal in width, the posterior being longer than the anterior; from the latter, two arms branch off antero-laterally, so large as to give frequently the appearance of a tri-partite vesicle. These arms narrow to become the main lateral collecting tubes, which bend sharply forward around the germ cell mass, extend anteriorly for a third of the body length, and bend on themselves to return a little way before dividing into anterior and posterior collecting tubules. The anterior collecting tubule undoubtedly receives the capillaries from flame cells I, II, III, and IV; the exact connections of I and II were traced, but it is not known whether III and IV join separately or constitute a pair whose capillaries unite in a common

tubule (Fig. 1) before joining, as in *C. rhabdocaeca*, with the excretory system of which there are many similarities. The posterior collecting tubule in all probability drains V, VI, VII, and VIII in the body and IX and X in the tail; the fact that V and VI, as well as VII and VIII, lie close together seems to show that their capillaries may unite before entering the posterior collecting tubule. There is a small island of Cort, although it is not easily seen; it is located in a dilated portion of the posterior part of the excretory vesicle, at the junction of body and tail. From this point the caudal excretory tube runs posteriorly through the center of the tail-stem, embedding itself in a mass of cells where the furcae branch off; here it divides and passes down each furca to open on the dorsal edge, midway to the tip. These openings are simple, not having the slight enlargement and protrusion frequent in mid-furcal pores.

Either a rudimentary ventral sucker is present, or the reproductive organs are represented by two cell masses (Fig. 7). A poorly-defined group of cells, lying just behind the posterior pair of penetration gland cells and bounded posteriorly and laterally by the bladder and main lateral collecting tubes, forms the larger mass; the group of cells in this position, usually staining deeply with hematoxylins, has constantly been interpreted as a germ cell mass in furcocercous cercariae. Between the first and second pairs of penetration gland cells is another cell mass, quite different in shape and more definite in outline; the cells composing this mass are apparently identical with those of the posterior mass. Whether this is a proliferating cell mass representing a degenerate ventral sucker, or a germ cell mass, is not entirely clear; no connections between the two masses were observed. The same two cell aggregates were found in *C. hamata*.

The parthenitae are elongate sporocysts of relatively small diameter, so much tangled in the snail liver that it is practically impossible to dissect out one unbroken; the longest obtained measured almost 1 cm. in length, varying in diameter from a few  $\mu$  to 200  $\mu$  (Fig. 18). Both those containing only very young germ balls and those containing mature cercariae are very motile, especially the free ends which project from the liver. The cercariae develop in batches, with constrictions between. The lumen is continuous throughout the entire length, although at the points of constriction it is so narrow that, in spite of rapid surging back and forth, it is likely that the groups remain separate while undergoing development. The free end is tapering and bluntly rounded, the most anterior part being translucent and free from pigment granules. Following this short region there is a considerable amount of yellow and orange pigment, and at a short distance from the anterior end are found the lips of a birth-pore (Fig. 2). The emergence of one cercaria was observed.

Of a collection of ninety-seven *Physa gyrina* on September 18, 1922, from the Drainage Ditch, Urbana, two were infested; on November 4,

one-half mile farther up the ditch, twelve in 177 were infested. The sizes of these fourteen snails varied from 11 mm. to 16 mm., greatest length of shell.

### CERCARIA HAMATA MILLER 1923

[Figs. 9-16]

Host, *Planorbis trivolvis*

Locality, Urbana, Illinois (Drainage Ditch)

Occasion, three times, September to November, 1922

This cercaria is similar in many respects to *C. multicellulata*, but may easily be distinguished from it by the absence of eye-spots; the figures for the latter may be used to show certain points of structure. *C. hamata* is also strikingly like *C. rhabdocaeca* Faust and may be identical with it, although there are certain differences, and some structures in the former which are not included in the description of the latter. The general form of locomotion in *C. hamata* and *C. multicellulata* is the same, but with a hand lens it is observed that in the case of the former the anterior part of the body is bent toward the ventral surface in a hook-shape when the cercaria is sinking through the water.

Sizes under various conditions are: under a cover glass but free-moving, body, 207  $\mu$  by 41  $\mu$ , tail-stem, 276  $\mu$ , furca 276  $\mu$ ; mounted in Canada balsam (average), body 179  $\mu$  by 28  $\mu$ , tail-stem 248  $\mu$ , furca 198  $\mu$ . It will be noted that in the process of making permanent mounts the furcae shrink more than the tail-stem.

Although body shape is not a reliable criterion for specific differences, *C. hamata* and *C. rhabdocaeca* differ in this regard. The sides of the body of the former are parallel and its diameter is not greater than that of the tail-stem; also a shape is never exhibited such as Faust has shown for the latter cercaria. On the contrary, the body sometimes bulges anteriorly during contraction, and the posterior part never increases much in diameter. All of the measurements of the body are greater than those given for *C. rhabdocaeca*. The two forms differ also in the form of the anterior organ; in Faust's species it is described as "oral sucker pyriform, with larger end directed inward." *C. hamata* has its anterior organ in the shape of a short oval, and while under cover glass pressure or in permanent mounts (Fig. 12) it may be somewhat pyriform, it never appears as Faust figured for *C. rhabdocaeca*. The spination is similar to that of *C. multicellulata*. In both *C. hamata* and *C. multicellulata* the tail-stem is attached terminally and presents the same annulated appearance; it also has a constant diameter throughout; in these characters both species differ from *C. rhabdocaeca*, the tail-stem of which tapers markedly, and shows no annulations.

Practically the entire lumen of the tail-stem of *C. hamata* is filled with caudal gland cells, which are therefore not so clearly defined as in *C. multicellulata*; they have the same clear, homogeneous appearance, slightly yellow, and with transparent nuclei. Sewell's description of short lateral branches of the caudal excretory tube of *C. indica* XXVII, also for *C. indica* II, is thought by the present author to be a misinterpretation of the boundaries of contiguous caudal gland cells; his records are the only ones of such lateral branches. The three longifurcate forms under discussion here are united in the absence of spines on the tail-stem, in contrast to the presence of a number of small, backward-pointing spines with which all four Indian representatives of the brevifurcate monostomes are furnished (*C. indica* IX, XIII, XXXIX, LV). *C. hamata* has four muscle bands in the tail (Fig. 10), and sensory hairs like those reported for *C. multicellulata*, relatively longer, and more numerous, about fifteen on each side; these have not been noted for any brevifurcate cercaria. These two forms have spines on the furcae; they were not reported for *C. rhabdocaeca*. *C. hamata* does not have thin furcal edges; *C. multicellulata* is the only one which has them.

Various degrees of development of the alimentary canal are represented; *C. multicellulata* shows only a trace of a narrow tube posterior to the anterior organ, although it is supposed that a pharynx is present, but is masked by the small parenchyme cells. *C. rhabdocaeca* was shown with a relatively wide prepharynx, slightly muscular pharynx, short inconspicuous esophagus, and single median cecum extending backward almost to the level of the first penetration gland. *C. hamata* has a capillary prepharynx, 10  $\mu$  long, and esophagus and cecum are represented by a pyriform vesicle behind the weakly muscular pharynx; the pharynx is 10  $\mu$  wide.

The number of penetration glands in the three North American species is the same, although their locations are somewhat different. In both *C. multicellulata* and *C. hamata* the anterior cell mass (rudimentary ventral sucker or germ cell mass) definitely separates the six gland cells into two groups. In the former species two gland cells are constantly anterior and four posterior to it; in the latter the distribution is not so regular, as in some individuals either two or three cells may compose the anterior set, and not infrequently one is also very clearly lateral to the germ cells, leaving only two posterior. In both species the coarsely granular protoplasm of these cells readily stains with neutral red in the living animal and is eosinophilic in sections (Fig. 16). In *C. rhabdocaeca* there is a single group of six contiguous cells. In *C. hamata* the penetration gland ducts from the two sides run through the center of the body, almost contiguous for the greater part of their length; here they are small and difficult to see individually. They diverge just behind the pharynx and enter the anterior organ, where they expand greatly so that their number and location are more

readily determined (Fig. 9). Associated with the gland duct openings is a group of about twelve small solid piercing spines which point forward, and which are arranged in a crescent around the dorsal side of the mouth opening. These spines are also solid in *C. multicellulata*, while in *C. rhabdoceca* they are hollow.

The excretory vesicle is a bipartite structure (Fig. 12), the anterior part being somewhat larger in all dimensions than the posterior. It is about one-fifth as wide as the part of the body in which it is situated. The lateral arms branch off without conspicuous enlargement, bend around the large germ-cell mass, and continue forward as the main lateral collecting tubes. A very small island of Cort is present. The openings of the caudal excretory tube branches are in the mid-furcal region. As in *C. multicellulata*, observation of details is very difficult, and while the locations of all body and tail-stem flame cells were made out, the connections of the capillaries with the larger tubules have not been determined. The figures for *C. multicellulata* serve equally well for the excretory system, except that in *C. hamata* the bending of the main lateral collecting tube is somewhat more anterior. In both species this reflexed tube is very clear; it is not shown in the figure for *C. rhabdoceca*, in which there is no obvious division of the main lateral collecting tube into anterior and posterior collecting tubules. It is likely that both *C. multicellulata* and *C. hamata* possess ciliated areas in the main lateral collecting tubes near the entrance of the anterior and posterior collecting tubules; several times, at the moment when a cercaria was going to pieces due to cover glass pressure, a flickering was noted lateral to the anterior cell mass in each species. The flame cells in the tail-stem of *C. hamata* are very small and are seen only with difficulty.

There are two large cell masses, consisting of a large number of small, deeply staining cells, similar in size and location to those of *C. multicellulata*. There are some indications of lateral connections between the two groups of cells, and also of lateral extensions forward from the anterior mass which meet in a median plane; thus the whole would form a figure eight. Whether these are both germ cell masses or the anterior one represents a rudimentary sucker has not been decided. These conspicuous cell masses were not described for *C. rhabdoceca*; Faust mentioned a few large germ cells as lying ventral to the bladder.

The parthenitae are long thread-like sporocysts (Fig. 11), not differing markedly from those of *C. multicellulata*. Bright yellow pigment granules are seen by reflected light, and examination under higher powers, with transmitted light, reveals the presence of other orange-colored spots. Waves of contraction, beginning at one end and passing through the entire length, were observed in sporocysts taken from the digestive gland soon after killing the snail. Puncture of the liver after careful removal of the shell results in a very active waving about on the part of protruding sporo-

cysts, even those containing very young germ balls. A birth-pore is present (Fig. 14).

*C. hamata* was found in one out of sixty specimens of *Planorbis trivolvis* from the drainage ditch, Crystal Lake Park, Urbana, collected September 25, 1922. On October 26 one *P. trivolvis* in 101 from the same location was infested. On November 4, one-half mile farther up the ditch, a collection of eleven of the same species yielded a single infection.

## CLASSIFICATION

There are at present upwards of one hundred furcocercous cercariae more or less fully described. It does not seem possible to devise a scheme of classification, upon either a natural or an artificial basis, which will include all forms; it is especially difficult to dispose of those for which only external characters are known, since they can not be placed except on the basis of general similarities to other completely described cercariae. The classification which the author proposes is preceded by a discussion of other recent ones.

The three groups which Cort (1917) established to contain six furcocercous cercariae were defined in the discussion of his paper in the historical section. He studied the homologies of the excretory systems of these larvae, and stated that his work had convinced him that "a more complete knowledge of this system will do much to clear up relationships and to establish natural families. Also an increased knowledge of the excretory systems of little known types of cercariae will be of great help in solving life-histories by suggesting the groups of adults to which such forms belong. In certain cases the close relationship of two cercariae may be shown by comparisons of their excretory systems, when on account of differing degrees of development of adaptive larval characters they superficially appear to be very different." Because only six fully described larvae were available for classification, Cort's scheme is too limited to allow the inclusion of all forms now known.

Sewell's classification (1922) is the result of a consideration of all well-described furcocercous larvae, including the monostomes. Although he recognized that these last are more closely related to distome furcocercous than to other monostome cercariae, nevertheless he considered them quite apart from the distome forms. No pharyngeal monostomes, other than those in the peculiar *Vivax* group, were known at the time of publication of his paper; he divided the monostome larvae into the *Lophocerca* group, with furcae shorter than one-half the length of the tail-stem and with a mid-dorsal body fin-fold, and the *Lophoides* group, the single member of which has relatively long furcae and no body fin-fold. For the distomes Sewell modified Cort's (1917) grouping to form the basis of his system of classification embracing a much larger number of forms. He united the first two groups of Cort into Group 1, and divided Cort's third into two, Group 2 and Group 3. Group 1 of Sewell, the brevifurcate apharyngeal distomes, was divided into two series mainly on the basis of presence or



absence of hollow piercing spines, and of presence or absence of fin-folds on the furcal rami; each series was further divided into subgroups, on the basis of the complexity of the excretory system pattern. The longifurcate distomes, Group 2, were divided into a pharyngeal and an apharyngeal series, the latter based on a single new species, *C. indica* XXII; three subgroups of the pharyngeal larvae were created, chiefly on the basis of the excretory system pattern, each to contain a single well-described larva. Group 3 was formed to contain *C. vivax* and two new species of longifurcate pharyngeal monostomes having the same peculiar type of excretory system. A number of larvae could not be included in his classification, largely because of incomplete descriptions.

Faust (1924) presented a scheme of classification for digenetic trematodes, mostly larvae, in which each ultimate group contains those forms whose excretory system formulae may be elaborated from a basic group formula. The furcocercous cercariae are placed together in the ninth subdivision under Distome Cercariae; furcocercous monostomes are included here also. The importance of the excretory system for the establishment of natural groups has already been stressed by Cort (1917), and discussed in some detail by Faust (1919b, c, d). In the paper now being considered Faust places still greater emphasis upon this system; he states (p. 261):

A study of the larval characters of the trematodes for some years has brought me to the conclusion that there is only one common system carried over from the cercaria to the adult, which is sufficiently definite and conservative as to be utilizable for purposes of group identification. That system is the excretory system. The more work that is done in this system, the more indicative it is of possessing value as a natural basis of classification, and the more evident is the artificiality of some of Lühe's groupings of larval forms and of the equal artificiality of some of the families of adult trematodes that have been created. While the study of adult correlations with known larval forms is still in its infancy, it is not too much to state that all members of a natural adult group possess the same basic excretory pattern.

This correspondence of close relationship with identical excretory systems has already been pointed out for the larvae of the three human schistosomes; furthermore, Faust and Meleney (1924) have shown that the excretory system in the post-larval stages of *Schistosoma japonicum*, the only species known in this respect, is a regular elaboration from that system in the cercaria.

Among the furcocercous cercariae about half of the groups had been established by Sewell; to some Faust added other larvae, and also set up new groups to contain one or more forms. A fundamental formula, with possible elaborations worked out *a priori*, was used, and it was found that the groups fitted into this formulary scheme, leaving very few gaps. However, the present author finds that certain of these groups are not homogeneous. In the Ocellata group are placed *C. ocellata*, with seven pairs of flame cells, arrangement unknown, *C. indica* XXV with five pairs, *C. indica*

XXXVI with four pairs observed and the possibility of a fifth pair, and *C. bilharsiiella*, of which nothing is known of the excretory system and practically nothing of the general morphology. Furthermore, identical formulae are given in two instances for widely separated groups; thus, that for the *furcicauda* group is the same as for the *burli* group (although in the latter it does not include the flame cells in the tail-stem); also the Baiswan group in one place, and the *emarginatae* and *telis* groups in another, are given identical formulae. This raises the question as to where a new species with either of these formulae would be placed; if general structural similarity is to be taken into account in these instances, it is difficult to see why *C. douthitti* and *C. elephantis* are placed together, since they are quite dissimilar in general organization (Miller, 1924). *C. pseudo-vivax* nov. sp. and *C. divaricata* nov. sp. were placed in the same group with *C. vivax*, although a complex excretory system of the Vivax type is not described for either.

Faust states (p. 263) that "the forms included in this table are by no means exhaustive, but no well-described species has been omitted simply because it does not fit into the scheme proposed." The present author sees no reason why *C. indica* IX, *C. indica* XLVII, *C. indica* LV, *C. bombayensis* no. 8, and *C. bombayensis* no. 9 were not included. Although in one of these species, *C. indica* XLVII, the exact connections of the flame cell capillaries are not shown, the same is true for *C. indica* XXXVI, which is included in the *ocellata* group.

The position held throughout as to the significance of the excretory system formulae of larvae must be based on the assumption that the elaboration into the system of the adult will proceed with regular divisions of the flame cells of the larva, otherwise the similarities of larval patterns would be of less value. The post-larval development has been followed in only one species of furcocercous cercariae, the cercaria of *Schistosoma japonicum*; in an early agamodistome stage of this species the posterior flame-cell in the body divided and re-established the condition of two flame cells in both anterior and posterior groups, thus compensating for the loss of the flame-cell in the discarded tail. From this it would seem that some flame-cells of the cercaria might have potentialities for more rapid division such that the pattern of the adult worm could not be predicted. That this may be the case is also indicated by the unequal development in some larvae of the anterior and posterior collecting tubule systems, although presumably each started with a single flame-cell. Furthermore, the fact that certain larvae, including *C. robusticauda* and *C. gigas*, have one or more flame-cells considerably larger than the others may indicate that these cells are about ready to divide; but whether they will dichotomize once or twice in a post-larval stage before the other cells do so cannot be predicted. It is extremely important that the excretory system pattern be worked out for the early post-larval stages of a number of fureocercous cercariae; unhappily only a

few life histories are known and so the materials for such studies are limited.

A fact which makes the use of the excretory system not very feasible, at least for practical purposes, is the great difficulty with which the pattern is determined. Cort, Faust and others have called attention to the tediousness of the study involved, and their experiences are born out by the studies of the present author on more than forty larval species. It is reasonably certain that the patterns described for a number of cercariae will have to be revised when these species are restudied; a mistake in locating the point at which any flame-cell capillary empties into the lateral collecting tubule will change the formula. Where the figure does not clearly show the connections, it may be impossible to decide what formula would represent the actual conditions.

In the scheme to be presented below the presence or absence of a pharynx is the first consideration for the division of the furcocercous larvae into two main groups; it is held that this character is of more significance than the presence or absence of a ventral sucker. This view is supported by Stunkard's (1923) studies on adult blood-inhabiting trematodes from reptiles, and his discussion of the relationships of these forms in fishes, reptiles, birds and mammals, a discussion in part previously taken up by Odhner (1912) and Ward (1921). These studies indicate that the blood flukes constitute a natural group. Two of the three families, the Schistosomatidae and the Spirorchidae, include forms which in the older classification would have been placed in the widely separate groups of Monostomes and Distomes. As all of these adults lack muscular pharynges, it would seem that the presence or absence of a pharynx is of great significance, while the possession or lack of a ventral sucker is relatively unimportant. Numerous other studies have shown that the monostomes were probably derived from the distomes by a gradual loss of the ventral sucker. Furthermore, some pharyngeal furcocercous larvae are now known to develop into members of the Holostomata, all of which possess pharynges. Accordingly, in the classification in this paper a division is first made between the pharyngeal and the apharyngeal forms, thus giving much more emphasis to this character than Sewell did; each of these groups is then further divided into brevifurcate and longifurcate larvae; and the monostome and distome members of each of the four resulting groups are separately considered.

An attempt has been made to include all furcocercous larvae for which there are adequate descriptions. As relatively few are described with respect to the exact pattern of the excretory system, all other points of morphology have been taken into consideration; even then it has been necessary to place many cercariae in a separate list of unclassified forms. If Faust's emphasis on the excretory system as the best criterion for the

formation of natural groups were strictly followed, a number of larvae would be otherwise allocated in the scheme. To express the degree of development of the excretory system, which is taken into account in the formation of the final groups, the formula used by Sewell has been employed with a slight modification; for example, the formula for the cercaria of *Schistosoma japonicum* is  $2 \times 3 (+1)$ , where two represents the two sides of the body, three, the number of flame-cells in one lateral half of the body, and,  $(+1)$ , the flame cell in one lateral half of the tail.

By far the greater number of the apharyngeal larvae have furcae which are shorter than one-half the tail-stem length; and the opposite is true of the pharyngeal forms, in which thirty-eight out of forty-one are longifurcate, with furcae approximately equal to, or in some cases longer than the tail-stem. The brevifurcate and longifurcate larvae differ in other characters than the relative lengths of furcae and tail-stem, although the terms are retained as convenient designations for the groups. They are compared below.

#### BREVI-FURCATE LARVAE

Furcae usually less than one-half the tail-stem length; frequently sharply delimited from the tail-stem.

Tail-stem diameter less than that of body; usually attached somewhat ventrally, sometimes decidedly so, such that a dorso-ventral mount is rare.

Furcal fin-folds sometimes present.

Body frequently very hyaline.

Eye-spots may be present.

Anterior organ a very highly modified oral sucker, with anterior thin-walled and posterior muscular portions; head gland usually present.

Ventral sucker usually much smaller in diameter than anterior organ; very protrusible and often held protruded.

Penetration glands very large; frequently divided into anterior coarsely granular and posterior finely granular cells.

Penetration gland duct openings frequently capped by hollow piercing spines.

Excretory openings at tips of furcae. Never more than one pair of flame cells in proximal part of tail-stem.

#### LONGIFURCATE LARVAE

Furcae longer than one-half the tail-stem, sometimes exceeding it; usually not sharply delimited.

Tail-stem diameter approximately equal to that of body when fully extended; attached terminally, dorso-ventral mount the usual one.

Furcal fin-folds absent.

Body usually crowded with small parenchyme cells.

Eye-spots usually absent.

Anterior organ less highly modified; cells which possibly represent a head gland present in but a few larvae.

Ventral sucker frequently large, in some cases of greater diameter than anterior organ.

Penetration glands small in proportion to body; no differentiation into anterior and posterior sets. Usually coarsely granular, and acidophilic in sections.

Solid piercing spines more frequent than hollow ones.

Excretory openings typically mid-furcal. Usually two pairs of tail-stem flame cells, seldom confined to a strictly proximal location.

Tail-stem wall usually provided with powerful longitudinal muscles. Caudal glands not conspicuous; when present, are not arranged in pairs along caudal excretory tube.

Tail-stem and furcae usually spined; no sensory hairs. Furcae almost cylindrical in some larvae.

Alimentary canal opens more or less ventrally as a capillary tube; ceca absent or at most very short.

Tail-stem wall frequently annulated; tail less powerful and more transparent. Conspicuous, more or less regularly paired caudal glands in a number of species.

Tail-stem usually devoid of spines; furcae may be spined; sensory hairs on the tail-stems of several larvae. Furcae never cylindrical, usually much flattened.

Alimentary canal usually opens terminally or subterminally; esophagus a fair-sized tube; ceca usually well-developed, frequently reaching almost to posterior end of body.

### APHARYNGEAL CERCARIAE

It is quite probable that some of the larvae included under this heading will be found, upon more careful study, to possess pharynges. Certain few larvae have been placed in sub-groups of the pharyngeal forms, in cases where other morphological characters strongly justify it, and point to the possible incompleteness of the description with respect to the pharynx.

#### APHARYNGEAL BREVIFURCATE CERCARIAE

This group has been most intensively studied, due to the fact that the larval forms of the human schistosomes are included here; accordingly the data for these cercariae permit the formation of a number of groups, on the basis of morphology in general, and in particular the pattern of the excretory system. The first division is into distomes and monostomes. These two groups are rather sharply divided from each other on the basis of several characters which will be discussed later.

#### APHARYNGEAL BREVIFURCATE DISTOME CERCARIAE

##### (Sewell's Group 1)

##### Group A (*japonicum* of Sewell)

Cercaria of *Schistosoma japonicum*

Cercaria of *Schistosoma haematobium*

Cercaria of *Schistosoma mansoni*

*Cercaria indica* XXX

Cercaria in Blacklock and Thompson 1924

It is now clear that all members of Group A have identical excretory system patterns; this consists of three pairs of flame cells in the body and one pair in the tail-stem, formula  $2 \times 3 (+1)$ . It has already been noted that the ciliated areas in the excretory vesicle arms were probably mistaken by previous workers for flame cells, thus accounting for the larger numbers

reported by Miyairi and Suzuki (1914), Ogata (1914) and Iturbe (1917). The same perfect agreement is not found in the penetration gland equipment. The varying number and character of these gland cells in the members of this group have been reviewed in numerous places in the historical section, as have also the conflicting statements concerning them within what is believed to be a single species. Either the observations have been faulty in some cases or there are more species of schistosomes than has been suspected.

Group B (*spindale* of Sewell, in part)

*Cercaria* B of Kemp

*Cercaria* of *Schistosoma spindale*

*Cercaria indica* XLVII

The last two species have four pairs of flame cells in the body and one pair in the tail-stem, formula  $2 \times 4 (+1)$ . The number of penetration glands is identical in these two also, namely two anterior pairs with coarsely granular protoplasm and three posterior pairs with finely granular protoplasm; in *C. indica* XLVII all five pairs are acidophilic, whereas the three posterior pairs of the cercaria of *S. spindale* are basophilic. *Cercaria* B is included here provisionally, chiefly on the basis of number and character of the penetration glands; the excretory system is unknown. This group has not been modified from Sewell, except by the addition of *Cercaria* B.

Several other forms, which have superficial characters of the schistosomes, but are not sufficiently known to be definitely placed, are included here for the sake of completeness. In the single figure given for it, *C. blanchardi* closely resembles the human schistosome larvae; Lutz (1919: 112) is of the opinion that da Silva studied the cercaria of *S. mansoni*. The cercaria in Leiper (1915, Fig. 46), was considered by him to be a schistosome larva; the figure shows it to have the general characteristics of these larvae. The cercaria in Manson-Bahr and Fairley (1920, Pl. III, Fig. 5), also seems to belong here; as already noted by Sewell, these authors were in error to suppose it to be the same as the form which Leiper provisionally called *C. bilharziella*, which has eye-spots, as these structures appear early in development and the figure given by them is of a mature cercaria, without eyespots. According to Cawston (1922c), *C. crispa* is a synonym of the cercaria of *S. haematobium*, and *C. spinosa* is possibly a synonym of the cercaria of *S. mansoni*.

Group C (*douthitti* of Sewell, in part)

*Cercaria douthitti*

*Cercaria* C of Kemp

*Cercaria* of *Schistosomatium pathlocopicum*

This group was created to contain *C. douthitti* and *C. elephantis*; these two larvae are different in certain respects and have been placed in separate groups (Miller, 1924). They differ in character and location of the penetration gland cells; and almost the entire posterior half of the body of *C. elephantis* is filled with a mass of cells not represented in *C. douthitti*.

*C. douthitti*, the type of the reconstituted group, has the flame-cell formula  $2 \times 5 (+1)$ . Its close resemblance to the cercaria of *Schistosomatium pathlocopicum*, except in the number of penetration gland cells, has been pointed out by Tanabe (1923); the excretory systems are identical in the number of flame cells. The knowledge of *Cercaria* C is confined to data from preserved material; it belongs here on the basis of general similarity.

Groups A, B and C differ chiefly in the complexity of the excretory system; the members have from three to five pairs of flame cells in the body. Probably all of these larvae will be included in the family Schistosomatidae.

Group D (*elvae*)

*Cercaria ocellata*

*Cercaria bombayensis* no. 19

*Cercaria elvae*

*Cercaria gigantea*

The reason for dissolving the Ocellata group of Sewell was stated under the description of *C. elvae*; here also was discussed the similarities of the four larvae placed in this group. These forms are especially interesting in that they possess many characters of the schistosome cercariae, and yet differ in having much more elongate bodies, pigmented eye-spots, and possibly furcal fin-folds in *C. ocellata*; these are the only four brevifurcate larvae which do not fall strictly within the definition, but have furcae somewhat longer than one-half the tail-stem. Soparkar (1921a) suggested that *C. bombayensis* no. 19 "belongs probably to the 'Bilharziella' group of cercariae"; the present author knows of no evidence in support of this statement.

Group E (*bombayensis* no. 13)

*Cercaria bombayensis* no. 13

*Cercaria indica* XXV

*Cercaria wardi*

The morphological basis for grouping these forms together was discussed in detail under the description of *C. wardi*. *C. bombayensis* no. 8, an intermediate between the apharyngeal brevifurcate monostomes and distomes, will be discussed under the group of brevifurcate monostomes; it is somewhat similar to *C. indica* XXV.

## Group F (Wynaad)

*Cercaria indica* XXXVI

Although this larva is in general like the members of Group E, it is here tentatively held as the representative of another group; this is partly because of the lack of the so-called posterior mucin gland, of unknown function and unique to the three members of Group E. Furthermore, it possesses a large number of small penetration gland cells, in two differentiated sets; and lacks a head gland, found in Group E larvae.

Group G (*elephantis*)*Cercaria elephantis**Cercaria echinocauda*

*C. elephantis* was placed by Sewell in the Douthitti group, and *C. echinocauda* in the Gigas group. The excretory formula is known for *C. elephantis* only,  $2 \times 5(+1)$ . The author studied living material of this species, collected from the same region of Michigan as was Cort's material; it was discovered that in addition to the numerous small gland cells which distend the posterior part of the body, designated as cephalic glands (Cort, 1917:53), there are also two distinct sets of penetration gland cells. Five pairs are centered around the ventral sucker; three pairs of small cells are anterior to two pairs of larger cells. Study of some alcoholic material of *C. echinocauda* (by Miller, 1924) revealed the presence of the same sort of a posterior cell mass as is found in *C. elephantis*; the number, location and relative size of the two sets of penetration glands are also the same.

Group H (*gigas* of Sewell, in part)*Cercaria gigas*

The unique type of excretory system reported for this larva shows that it is very different from any other described form. However, it does not depart in other of the important characters as far from the Group F or G types as might be concluded from Faust's original description (1918a). The author's material of *C. gigas*, as well as co-type slides in the collection of Professor Ward, shows that an alimentary canal like that described for *C. wardi* is present, contrary to Faust's statement that pharynx, esophagus and ceca are wanting. There are five pairs of large penetration gland cells anterior to the germ-cell mass, and two pairs posterior to it. Sewell regarded *C. gigas* as the highest stage of development in his Group 1, representing the culmination of alimentary canal retrogression and excretory system development. His conclusion may be justified on the basis of the large number of flame-cells; but the larva is not an example of extreme degeneration of the alimentary canal.



## Miscellaneous group

*Cercaria bilharziella**Cercaria oculata**Cercaria parvoculata**Cercaria patialensis*

These larvae complete the list of those known to be apharyngeal brevifurcate distomes. The exact positions of the first three cannot be determined until more complete descriptions are available. All four have pigmented eye-spots, and the last three are reported to develop in rediae. *C. patialensis* has a unique excretory system and tail-stem, and has the highest degree of development of the genital system found in the furcocercous larvae. It cannot now be placed in relation to any other known form.

A key for the separation of these sub-groups of the apharyngeal brevifurcate distomes has been published (Miller, 1923).

## APHARYNGEAL BREVIFURCATE MONOSTOME CERCARIAE

Only two of these forms were known to the earlier workers: *C. cristata* and *C. microcristata*. To these are to be added *C. indica* IX, XIII, XXXIX, and LV, *C. bombayensis* no. 8, and the cercaria of *Sanguinicola inermis*. No members have been reported from the fresh waters of this country; one unnamed marine species has been described by Linton (1915). As the present author has no personal acquaintance with these forms, the attempt to critically consider Sewell's disposition of them will be based entirely on a study of the literature. His analysis took into account all species except the cercaria of *Sanguinicola inermis*, and incorrectly included *C. varicans*, which is clearly figured by Abildgaard as a longifurcate larva, with furcae almost if not quite as long as the tail-stem. Sewell took the group name *Lophocerca* from Lühe; the most striking features of these larvae are the presence of a body crest and the absence of any trace of pharynx or intestine. The group can not be subdivided, as Sewell's species are the only ones for which the excretory and penetration gland systems are known.

The original account of *C. cristata* has been studied, as have also the numerous subsequent references to it by other workers; it seems probable, as Sewell suggested, that more than one larva has been included under this specific name. Because of its inadequate description Scheuring concluded that the identity of this species with the cercaria of *Sanguinicola inermis* was doubtful. Ercolani described *C. microcristata* as similar to *C. cristata* except for smaller size. Both *C. bombayensis* no. 8 and the cercaria of *Sanguinicola inermis* have been described in sufficient detail so that they could readily be recognized. As Sewell noted, the former of these two is intermediate between the monostomes and distomes, both in the presence of a small body crest and of a group of cells probably representing a rudi-

mentary ventral sucker. The descriptions of the four new Indian species contribute many details of structure not previously known for brevifurcate monostomes; Sewell believes that *C. indica* XIII is only questionably distinct from *C. cristata*.

Lophocerca Group of Sewell, in part

*Cercaria cristata*

*Cercaria microcristata*

*Cercaria* of *Sanguinicola inermis*

*Cercaria bombayensis* no. 8

*Cercaria indica* IX

*Cercaria indica* XIII

*Cercaria indica* XXXIX

*Cercaria indica* LV

Here are briefly recapitulated some of the characters enumerated by Sewell: the body is provided with a dorsal longitudinal crest; a definite oral sucker is absent, and the anterior end forms a conical protrusible and retractile snout; there is no trace of pharynx or intestine; where the excretory system has been worked out, the formula is  $2 \times 3 (+0)$ ; development is in small rounded or oval sporocysts. It is to be noted that there are no flame-cells in the tail-stem of these larvae, which makes them unique among furcocercous forms.

APHARYNGEAL LONGIFURCATE CERCARIAE

In general these larvae resemble the pharyngeal longifurcates more closely than other apharyngeal larvae, either distomes or monostomes. Nevertheless, it is thought that the presence or absence of a pharynx is of more significance than similarity in larval characters. The few cercariae under this heading are not all well-described; they do not seem to form a homogeneous group, and the disposition of them into sub-groups will have to be postponed until more species are described.

Apharyngeal Longifurcate Distome Cercariae

*Cercaria gracillima*

*Cercaria tuberistoma*

*Cercaria gladii*

*Cercaria minima*

*Cercaria indica* XXII

*Cercaria* in Lagrange 1923:175

Apharyngeal Longifurcate Monostome Cercariae

*Cercaria indica* XXVII

This is the only unquestionable representative of this group. Repeated studies on *C. multicellulata* failed to show any trace of a pharynx, but observation was hindered by the numerous refractile parenchyme cells crowding the body; and this larva is so strikingly similar in most respects to *C. hamata*, which has a definite pharynx, that it has been classed with the pharyngeal forms. *C. indica* XXVII is not very similar to any of the six apharyngeal longifurcate distomes, from which group it would presumably have been derived by loss of the ventral sucker. Its resemblance to the schistosomes in two characters was pointed out by Sewell, that is, the presence of an anterior protrusible penetrating organ and an exactly similar excretory system.

### PHARYNGEAL CERCARIAE

Approximately one-half of the furcocercous cercariae are known to possess pharyngeal sphincters. The first division of these, as with the apharyngeal cercariae, is made between the longifurcate forms, of which there are thirty-eight, and the three brevifurcate forms.

#### PHARYNGEAL BREVIFURCATE CERCARIAE

##### Pharyngeal Brevifurcate Distome Cercariae

*Cercaria scripta*

*Cercaria parthenicola*

*Cercaria octadena*

Until more complete accounts of these forms are available, including analyses of the excretory system patterns in living material, little can be said of their relationships; the first two were reported to develop in rediae. It is surprising that Faust believes *C. octadena* to be the larva of *Schistosoma bovis*; he figured it with a small pharynx. This is the only recent account which assigns a pharyngeal larva to the family Schistosomatidae.

##### Pharyngeal Brevifurcate Monostome Cercariae

No representatives

#### PHARYNGEAL LONGIFURCATE CERCARIAE

This is the largest group of furcocercous larvae, and the one concerning the adult affinities of which nothing was known until the work of Ruszkowski, Lutz, and Szidat. Many of the members are very incompletely described, and relatively few are known with respect to the excretory system pattern. This system was not described in the cercaria of *Hemistomum alatum*; it was only partially figured by Szidat in *Cercaria* A, which develops into *Tetracotyle typica*. Hence other cercariae for which the complete excretory patterns are known cannot be placed in relation to these known holostome larvae.

PHARYNGEAL LONGIFURCATE DISTOME CERCARIAE  
(Sewell's Group 2, Series 1)

In his consideration of these forms Sewell created three sub-groups, each to contain a single cercaria; five other incompletely described larvae were referred either tentatively to one of these sub-groups, or to the series. At the present time there are thirty-one of these cercariae, and probably other members which are classed among the partially known and unplaced forms. The penetration glands have been described in twenty-one larvae, and the entire excretory system is known for eleven species, with incomplete descriptions for five more. Only sixteen larvae have been described with respect to both systems. In spite of this great increase over the number considered by Sewell, the present author has not been able to establish a satisfactory scheme of relationships, due to the paucity of morphological data. The great diversity, even in the eleven fully described species, of flame cell number and of nature and number of the penetration glands makes it almost impossible to arrange them in any feasible systematic scheme. The author has been unable to find correlation between any two of the following: body, tail-stem and furcal lengths; number and arrangement of flame cells; number, location in body, and character of penetration gland cells; type of alimentary canal; size and location of ventral sucker.

The following belong here; formulae for the excretory system are included.

*Cercaria* A (Szidat)

"	<i>aculeata</i>	
"	B (Szidat)	
"	<i>bdello cystis</i>	
"	<i>bombayensis</i> no. 9	2×10(+2)
"	<i>burti</i>	2×6(+2)
"	C (Szidat)	
"	<i>chrysenterica</i>	2×7(+2)
"	<i>divaricata</i>	
"	<i>douglasi</i>	2×5(+2)
"	<i>emarginatae</i>	2×5(+2)
"	<i>fissicauda</i>	
"	<i>furcicauda</i>	2×5(+1)
"	<i>gracilis</i>	
"	<i>gyrinipeta</i>	

*Cercaria* of *Hemistomum alatum*

"	in Hesse 1923	2×7(+2)
<i>Cercaria indica</i> I		2×5(+1)
" <i>indica</i> II		2×10(+2)

“ *letifera*

“ *longissima*

Cercaria in Manson-Bahr and Fairley (1920, Pl. III, Fig. 7)

*Cercaria minuta*

“ *molluscipeta*

“ *pseudo-vivax*

“ *quattuor-solenata*                      2×6(+2)

“ *redicola*

“ *robusticauda*                              2×6(+1)

“ *secobii*

“ *tenuis*                                        2×5(+2)

#### PHARYNGEAL LONGIFURCATE MONOSTOME CERCARIAE

These larvae fall into two closely circumscribed groups. The first is the one which Sewell set up to contain *C. vivax* and two new species which he described. All members have a unique type of excretory system in the body, and three pairs of flame-cells in the tail-stem; in no case do the numerous penetration gland cells extend into the posterior half of the body. Only one larva, *C. leptoderma*, is to be added to this group; neither *C. pseudo-vivax* nor the cercaria in Leiper and Atkinson 1915 have been shown to have the highly developed excretory system, although Faust has included the former in the *Vivax* group. *C. indica* XXXIII (*tetis* group of Sewell) has the same unique arrangement of collecting tubules in the body, but only five pairs of flame-cells in the body and two pairs in the tail-stem; it probably is the sole known representative of a sub-group. Although *C. vivax* possesses a ventral sucker, this structure is either entirely lacking or represented by a mass of cells in the other members. It would seem that the very unique development of the excretory system, together with the three pairs of flame-cells in the tail-stem, is of more significance than the presence or absence of a ventral sucker.

Vivax group (Sewell's Group 3)

*Cercaria vivax*

*Cercaria indica* XV

*Cercaria indica* LVIII

*Cercaria leptoderma*

Tetis group of Sewell

*Cercaria indica* XXXIII

The remaining group contains *C. rhabdocaeca*, *C. hamata*, and *C. multi-cellulata*. As noted above, a pharynx was not observed in the last-mentioned larva. It is included here because of many striking similarities, which have been discussed under the description of *C. hamata*. All three

species have eight pairs of flame cells in the body and two pairs in the tail-stem.

Rhabdocaeca group

*Cercaria rhabdocaeca*

*Cercaria hamata*

*Cercaria multicellulata*

FURCOCERCOUS CERCARIAE OF UNCERTAIN POSITION

The following forms have been incompletely described with respect to the presence of a pharynx, the character of the excretory system, or the penetration glands. In some cases, as where a microphotograph is given without description in the text, it is not clear whether a ventral sucker is present. The probable groupings of all are given, on the basis of all known characters.

Brevifurcate Distomes

*Cercaria andoi*

*Cercaria* in Lagrange (1923:177); probably apharyngeal

*Cercaria* in Manson-Bahr and Fairley (1920, Pl. III, Fig. 5); probably apharyngeal

Brevifurcate Monostomes

*Cercaria senoi*

*Cercaria* in Lühe (1909:206)

Longifurcate Distomes

*Cercaria furcata*

" *inversa*

*Cercaria* in Lühe (1909:204)

" in Leiper and Atkinson (1915)

*Cercaria paludinarum*

" *pseudo-divaricata*

" *quieta*

" *shinchikuensis*

" *valdefissa*

Longifurcate Monostomes

*Cercaria varicans*,

Unknown

*Cercaria bipartita*

*Cercaria* in Lagrange (1919)

*Cercaria ocellifera*; brevifurcate, probably apharyngeal

## CHECK-LIST OF FURCOCERCOUS CERCARIAE

The following list contains the specific names and references to the original descriptions of all furcocercous cercariae, both fresh-water and marine; the latter, included for the sake of completeness, are separately grouped at the end. The synonyms and descriptive modifications of *Cercaria* are also given. In cases where the original descriptions are very brief or entirely inadequate, and a later study has been comprehensive, this latter reference is also given.

## FRESH WATER SPECIES

- Cercaria* A in Kobayashi 1922:14, for *Cercaria* of Seno 1903; renamed *C. senoi* in Faust 1924:296
- " A in Szidat 1924:301-303; text-fig. 1
- " *aculeata* in Ercolani 1882:47; Pl. 1, figs. 42-46
- " sp. IX in Ando 1918:616; renamed *Cercaria* C in Kobayashi 1922:14; renamed *C. pseudodivaricata* in Faust 1924:296
- " sp. X in Ando 1918:617; renamed *Cercaria* B in Kobayashi 1922:14; renamed *C. andoi* in Faust 1924:296
- " *andoi* in Faust 1924:296, for *Cercaria* sp. X in Ando 1918:617 and *Cercaria* B in Kobayashi 1922:14
- " B in Kemp 1921:231-232; text-fig. 1, d, e
- " B in Kobayashi 1922:14, for *Cercaria* sp. X in Ando 1918:617; renamed *C. andoi* in Faust 1924:296
- " B in Szidat 1924:303; text-fig. 2
- " VI in von Baer 1827:627; Pl. 31, figs. 6a, 6b; synonym of *Malleolus furcatus* in Diesing 1850:295; synonym of *C. furcata* in Moulinié 1856:168
- " *bdello cystis* on page 77, for *Dicranocercaria bdello cystis* in Lutz 1921:126
- " *bilharziella* in Leiper 1915:259
- " *bilharziellalunata* nom. nud., synonym of *C. oculata* according to Faust 1920b:216
- " *bipartita* in Sonsino 1897:253
- " in Blacklock and Thompson 1924:212-220; 3 text-figs.
- " *blanchardi* in da Silva 1912:398-400; 3 figs.
- " *bombayensis* no. 8 in Soparkar 1921a:24-26; Pl. III, 4 figs.
- " *bombayensis* no. 9 in Soparkar 1921a:26-28; Pl. IV, 4 figs.
- " *bombayensis* no. 13 in Soparkar 1921a:29-30; Pl. V, 4 figs.
- " *bombayensis* no. 19 in Soparkar 1921a:30-32; Pl. VI, 3 figs.
- " *burti* in Miller 1923; in the present paper, page 41
- " C in Kemp 1921:232; text-fig. 1, f
- " C in Kobayashi 1922:14, for *Cercaria* sp. IX in Ando 1918:616; renamed *C. pseudo-divaricata* in Faust 1924:296
- " C in Szidat 1924:303-304; text-figs. 3a, 3b
- " *chrysen terica* in Miller 1923; in the present paper, page 47
- " *crispa* in Cawston 1920a:439, synonym of the cercaria of *Schistosoma haematobium* according to Cawston 1922c:247
- " *cristata* in LaValette St. George 1855:23; Pl. II, K

- " D in Kobayashi 1922:15, for *Cercaria* sp. XIV in Nakagawa 1915:116; renamed *C. paludinarum* in Faust 1924:296
- " *divaricata* in Faust 1924:256; Pl. II, fig. 12
- " *divaricauda* in Faust 1924:283; Table I, page 296; Table II, opp. page 298; error for *C. divaricata*
- " *douglasi* in Cort 1917:53-54; text-fig. 2, C
- " *douthilli* in Cort 1914:77-78; text-fig. 10; 1915:49-52; Pl. VII, figs. 55-64
- " E in Kobayashi 1922:15, for *Cercaria* sp. XV in Nakagawa 1915:116; renamed *C. shinchikuensis* in Faust 1924:296
- " *echinocauda* in O'Roke 1917:170-171; Pl. V, figs. 39-45; according to Miller 1924: 146-148; Pl. VI, figs. 4, 6
- " *elephantis* in Cort 1917:52-53
- " *elvae* in Miller 1923; in the present paper, page 30
- " *emarginatae* in Cort 1917:53; text-fig. 2, B
- " F in Kobayashi 1918:61; text-figs. 11, 12; 1922:15; Pl. IV, figs. 1, 2; renamed *C. parthenicola* in Faust 1924:296
- " *fissicauda* in La Valette St. George 1855:21; Pl. II, figs. VI and H
- " *furcata* in Nitzsch 1817:49; Pl. 2, figs. 12-18
- " *furcicauda* in Faust 1919c:336-337; text-fig. 6
- " G in Yoshida 1917:117; Pl. II, figs. 17, 18, text-fig. 11; in Kobayashi 1922:16; renamed *C. scripta* in Faust 1924:296
- " *gigantea* in Faust 1924:257; Pl. II, fig. 13
- " *gigas* in Faust 1918a:105-107; Pl. II, figs. 25-30
- " *gladii* in Cawston 1918a:96; according to Faust 1919a:164-165; Pl. XVIII, fig. 1
- " *gracilis* in La Valette St. George 1855:20; Pl. I, fig. XIII
- " *gracillima* in Faust 1917:122; Faust 1918:80; figs. 142-154, 161
- " *gyrinipeta* in the present paper, page 77, for *Dicranocercaria gyrinipeta* in Lutz 1921:126
- " H in Kobayashi 1922:16, for the cercaria of *Schistosoma japonicum* in Miyairi and Suzuki 1914
- " *hamata* in Miller 1923; in the present paper, page 55
- " of *Hemistomum alatum* in Ruszkowski 1922:237-250; 3 text-figs.
- " in Hesse 1923:227-231; 8 text-figs.
- " I in Kobayashi 1922:17, for *Cercaria* sp? in Suzuki and Nishio 1914; renamed *C. longissima* in Faust 1924:297
- " *indica* I in Sewell 1922:268-270; Pl. XXIX, figs. 1, 2
- " " II in Sewell 1922:271-274; Pl. XXIX, figs. 3, 4
- " " IX in Sewell 1922:47-50; Pl. IV, figs. 1, 3
- " " XIII in Sewell 1922:50-53; Pl. IV, figs. 3, 4
- " " XV in Sewell 1922:280-288; Pl. XXXI, figs. 1, 2
- " " XXII in Sewell 1922:276-278; Pl. XXX, figs. 1, 3
- " " XXV in Sewell 1922:260-262; Pl. XXVIII, figs. 1-3
- " " XXVII in Sewell 1922:59-61; Pl. V, fig. 3
- " " XXX in Sewell 1919:425; Pl. XXV; 1922:251-254; Pl. XXVII, figs. 1-3
- " " XXXIII in Sewell 1922:292-294; Pl. XXX, figs. 4, 5
- " " XXXVI in Sewell 1922:263-265; Pl. XXVIII, figs. 4, 5
- " " XXXIX in Sewell 1922:53-55; Pl. V, fig. 1
- " " XLVII in Sewell 1922:255-257; Pl. XXVII, figs. 4, 5
- " " LV in Sewell 1922:55-57; Pl. V, fig. 2
- " " LVIII in Sewell 1922:290-291; Pl. XXXI, fig. 3
- " *inversa* in O'Roke 1917:169-170; Pl. V, figs. 46-51
- " J in Kobayashi 1922:17; Pl. IV, figs. 3-5; renamed *C. redicola* in Faust 1924:297



- " sp. no. 1 in Lagrange 1919:386
- " in Lagrange 1923:175
- " in Lagrange 1923:177
- " in Leiper 1915, text-fig. 46; 1918:239, 241
- " in Leiper and Atkinson 1915:202; fig. 6
- " *leptoderma* in Faust 1922a:255-257; Pl. XXI, figs. 7-11
- " *letifera* in Fuhrmann 1916:389-393; Pl. I, figs. 1-8, 10
- " *longissima* in Faust 1924:297, for *Cercaria* sp? in Suzuki and Nishio 1914 and *Cercaria* I in Kobayashi 1922:17
- " in Lühe 1909:204
- " in Lühe 1909:206
- " in Manson-Bahr and Fairley 1920:54; Pl. III, fig. 5
- " in Manson-Bahr and Fairley 1920:54; Pl. III, fig. 7
- " *marcianae* in LaRue 1917:3; Pl. I, figs. 1, 2; synonym of *Agamodistomum marcianae* in Cort 1918a:130
- " *microcrinata* in Ercolani 1881:56-57; Pl. I, figs. 23-27
- " *minima* in Faust 1919:92, for *C. minor* Faust 1918a, preoccupied by Lebour 1912:424
- " *minor* in Faust 1918a:107-109; Pl. II, figs. 31-33; synonym of *C. minima* in Faust 1919:92
- " *minuta* in Ercolani 1882:46-47; Pl. I, figs. 1-6
- " *molluscipeta* in the present paper, page 77, for *Dicranocercaria molluscipeta* in Lutz 1921:126
- " *multicellulata* in Miller 1923; in the present paper, page 50
- " sp. XIV in Nakagawa 1915:116; fig. 14; renamed *Cercaria* D in Kobayashi 1922:15; renamed *C. paludinarum* in Faust 1924:296
- " sp. XV in Nakagawa 1915:116; fig. 15; renamed *Cercaria* E in Kobayashi 1922:15; renamed *C. shinchikuensis* in Faust 1924:296
- " *ocellata* in LaValette St. George 1855:22; Pl. II, fig. V
- " *ocellifera* in the present paper, page 73, for *Dicranocercaria ocellifera* in Lutz 1919: Pl. 41, figs. 64-66
- " *octadena* in Faust 1921d:11-12; Pl. III, fig. 1
- " *oculata* in Cawston 1917:132
- " *paludinarum* in Faust 1924:296, for *Cercaria* sp. XIV in Nakagawa 1915:116, and *Cercaria* D in Kobayashi 1918:15
- " *parthenicola* in Faust 1924:296, for *Cercaria* F in Kobayashi 1918:61
- " *parvoculata* in Cawston 1919a:401, according to Faust 1919a:165; Pl. XVIII, fig. 2
- " *patialensis* in Soparkar 1924:933-941; Pl. LXII, figs. 1-12
- " *pseudo-divaricata* in Faust 1924:296, for *Cercaria* sp. IX in Ando 1918:616, and *Cercaria* C in Kobayashi 1922:14
- " *pseudo-vivax* in Faust 1924:255; Pl. II, fig. 11
- " *quattuor-solenata* in Faust 1919c:337-338; text-fig. 8
- " *quieta* in O'Roke 1917:171-172; Pl. IV, figs. 32, 33, 37
- " *redicola* in Faust 1924:297, for *Cercaria* J in Kobayashi 1922:17
- " *rhabdocaeca* in Faust 1919c:338-339; text-fig. 9
- " *robusticauda* in Faust 1919c:337; text-fig. 7
- " of *Sanguinicola inermis* in Scheuring 1920:227; 1 text-fig.; Scheuring 1922:296-299; Pl. 23; fig. 12; text-fig. C
- " of *Schistosoma haematobium* in Leiper 1915:258; text-fig. 47; according to Faust 1920a:192-193; Pl. XV, figs. 1, 3; according to Bettencourt and da Silva 1922:1050; 1 text-fig.
- " of *Schistosoma japonicum* in Miyairi and Suzuki 1914:187-197; 1 fig.; according to Cort 1919:485-507; text-figs. 1-3

- " of *Schistosoma mansoni* in Leiper 1915:258; text-fig. 45; according to Faust 1920a: 192-193; Pl. XV, figs. 2, 5, 6; according to Khalil 1922: 27-34; text-figs. 1, 2
- " of *Schistosoma spindale* in Soparkar 1921:1-22; Pl. I, II
- " of *Schistosomatium pathlocopicum* in Tanabe 1923:183-186; Pl. XIV
- " *scripta* in Faust 1924:296, for *Cercaria* G in Yoshida 1917:117, and *Cercaria* G in Kobayashi 1922:16
- " *secobiana* in Cawston 1917:133; synonym of *C. secobii* in Cawston 1917b:91
- " *secobii* in Cawston 1915:1427; according to Faust 1921d:12; Pl. III, fig. 2
- " in Seno 1903:309; Pl. VII, figs. 2A, B; named *Cercaria* A in Kobayashi 1922:14; renamed *C. senoi* in Faust 1924:296
- " *senoi* in Faust 1924:296, for the cercaria in Seno 1903:309, and *Cercaria* A in Kobayashi 1922:14
- " *shinchikuensis* in Faust 1924:296, for *Cercaria* sp. XV in Nakagawa 1915:116 and *Cercaria* E in Kobayashi 1918:15
- " *spinosa* in Cawston 1919:189, synonym of the cercaria of *Schistosoma mansoni* (?) in Cawston 1922c:247
- " in Suzuki and Nishio 1914:587; 3 figs; named *Cercaria* I in Kobayashi 1922:17, renamed *C. longissima* in Faust 1924:297
- " *tenuis* in Miller 1923; in the present paper, page 45
- " *tuberistoma* in Faust 1917:123; 1918:82-83; Pl. IX, figs. 155-158
- " *valdefissa* in the present paper, page 77, for *Dicranocercaria valdefissa* in Lutz 1919:Pl. 41, figs. 67, 68
- " *varicans* in Abildgaard 1794:89; Pl. IIIa, figs. 1-4
- " *vivax* in Sonsino 1892:137; Pl. XVIII, fig. 3; according to Looss 1896:210-223; Pl. XV, figs. 162-177
- " *wardi* in Miller, 1923; in the present paper, page 35

## MARINE SPECIES

- Cercaria dichotoma* in Müller 1850; according to La Valette St. George 1855: Tab. II, fig. 1
- " *discursata* in Ssinitzin 1911:67; figs. 45-48
  - " of *Haplocladus minor*? in Odhner 1911b:105
  - " in Haswell 1902:497-511; Pls. 19, 20, figs. 1-31
  - " in Linton 1915:115-118; text-figs. 1-5
  - " in Linton 1915a:207-208; text-figs. 7, 8
  - " in Morgan 1891:1137-1139; 1 text-fig.
  - " *syndosymae* in Pelseeneer 1906; 172; Pl. IX, X, figs. 20-22

## SYNONYMS

- C. (Schisocerca) dichotoma* in Diesing 1858:265; synonym of *Cercaria dichotoma*  
*C. (Schisocerca) fissicauda* in Diesing 1858:265; synonym of *Cercaria fissicauda*  
*C. (Schisocerca) gracilis* in Diesing 1858:264; synonym of *Cercaria gracilis*  
*Cheilostomum varicans* in Diesing 1850:293; synonym of *Cercaria varicans*  
*Dicranocercaria bdilocystis* in Lutz 1921:126; synonym of *Cercaria bdilocystis*  
*Dicranocercaria gyrinipeta* in Lutz 1921:126; synonym of *Cercaria gyrinipeta*  
*Dicranocercaria molluscipeta* in Lutz 1921:126; synonym of *Cercaria molluscipeta*  
*Dicranocercaria ocellifera* in Lutz 1919:Pl. 41; synonym of *Cercaria ocellifera*  
*Dicranocercaria valdefissa* in Lutz 1919:Pl. 41; synonym of *Cercaria valdefissa*  
*Histrionellina fissicauda* in Diesing 1858:269; synonym of *Cercaria ocellata*  
*Lophocercaria fissicauda* in Diesing 1858:243; synonym of *Cercaria cristata*  
*Malleolus furcatus* in Ehrenberg 1838:465; synonym of *Cercaria furcata*  
*Schistocercaria*, proposed by Soparkar, 1921, for cercariae known to be the larval stages of schistosomes.

## DISCUSSION OF LIFE HISTORIES

Although brief references to the life history studies on furcocercous cercariae are included in the historical review, they are brought together here in order to sum up the present knowledge of the group in this field. Until recently the three species of human schistosome cercariae were practically the only larvae for which the adults were known. *Schistosoma japonicum* was the first which was shown to have as its larval stage a furcocercous cercaria (Miyairi and Suzuki, 1913, 1914). Leiper (1915) subsequently proved that both of the other human schistosomes, *S. haematobium* and *S. mansoni*, also developed directly from such larvae found in certain of the molluscs of Egypt. These findings exploded the theory Looss held persistently for so long, that adult schistosomes developed directly from miracidia without the intervention of an intermediate mollusc host. The life history of another of these forms, *S. spindale*, parasitic in cattle in India, has been experimentally demonstrated (Liston and Soparkar, 1918). Very recently the life cycle of a North American trematode, *Schistosomatium pathlocopicum*, a new genus and species of the family Schistosomatidae, has been worked out (Tanabe, 1923). The larva is a brevifurcate distome very similar to *Cercaria douthitti*; it has been experimentally shown to develop in laboratory rats. Thus five furcocercous cercariae, all brevifurcate distomes, are known to develop into members of the family Schistosomatidae, following direct penetration of epithelial surfaces of the final host.

Previous to this no complete life histories were known; brief notes on a few forms appear in the literature before 1913. In the case of *C. fissicauda* there is an indication of one stage in the life history. Blochmann (1910) noted that this cercaria penetrated and caused the death of several species of fish and of axolotl and salamander larvae, being found in large numbers in the freshly-examined brain, heart and heart blood. Experiments apparently were not carried on to determine whether the cercariae would develop further in any of these animals. Some unpublished observations of Looss on the life history of *Sanguinicola inermis* were included by Odhner (1911) as an addendum to his discussion of this trematode. Goldfish and carp in aquaria with *Lymnaea auricularia* harboring a furcocercous cercaria became infested in every case with large numbers of young worms, which were found in the mouth cavity and on the gills. In the carp only, these became sexually mature in the blood stream. Only one figure, without an accompanying description, was given for the larva, which is clearly a brevifurcate monostome; although Looss called it *C. cristata*. the information

given is not sufficient to establish its identity with this species. Scheuring has raised this question. The adult worms found were *Sanguinicola inermis*. In a parallel case to that of *C. fissicauda* above, *C. letifera* caused the death of five species of fish kept in small aquaria with the mollusc host (Fuhrmann, 1916); death was said to be due to hemorrhages and capillary obstruction caused by migrations of the larvae. Without further experimental proof, Fuhrmann supposed the intermediate host to be one or several species of fish, and the definitive host to be probably a piscivorous fish or bird.

The agamodistome stages of two cercariae were found in *Thamnophis marciana* and *T. eques* by LaRue (1917), who called them *Cercaria marcianae* and *C. vergrandis*. The first, more properly called *Agamodistomum marcianae*, was studied by Cort (1918); on the basis of its excretory and penetration gland systems he concluded that it is the agamodistome stage of a furcocercous cercaria, similar to but not identical with either *C. emarginatae* or *C. douglasi*.

The life history of *Sanguinicola inermis* has been experimentally worked out in detail by Scheuring (1920, 1922); although the larval form is very similar to *C. cristata*, Scheuring concluded that the identity of the two forms is doubtful. The larva reaches the blood stream of its final host, a fish, by direct penetration. The relationship of *Sanguinicola*, family Aporocotylidae, to the Spirorchidae and Schistosomatidae has been reviewed in the historical section of the present paper.

Several furcocercous cercariae from Brazil have been traced through all stages to tetracotyles, after penetration of an intermediate host; and these, when the proper final host was found by experimental feedings, developed into members of the genus *Strigea* (Lutz, 1921). In the cases of three new species, *Cercaria molluscipeta*, *C. gyrinipeta*, and *C. bdello cystis*, the first-named penetrated and continued development in snails, the second in tadpoles, and the third in leeches. One of the most interesting discoveries was that these cercariae do not immediately encyst in the tissues of the intermediate host, but pass a longer precystic stage free in the tissues, during which important structural modifications are undergone. The development of the genital system and the definitive form of the body does not take place until transfer into the final host.

The life history of an European member of the Holostomata *Hemistomum alatum*, has been experimentally determined by Ruszkowski (1922); he cultured the eggs and attempted to infest snails. The miracidia developed in several species of Planorbis, and elongate sporocysts and longifurcate distome cercariae were secured. The description of the latter is not sufficiently detailed to enable them to be placed in a classification scheme. Although the life cycle from cercaria to adult worm has not yet been traced, Ruszkowski's findings supplement those of Lutz on holostomid develop-

ment. It is now clear that the Holostomata develop from cercariae which have their origin in parthenitae in snails; these, so far as is known, are pharyngeal longifurcate distomes. The mode of development of this group, so long unknown, has now been experimentally determined.

*Cercaria vivax* may penetrate the skin and perhaps the digestive tube of certain tadpoles so rapidly, under experimental conditions, as to cause death in fifteen minutes (Brumpt, 1922); while the development was not followed out, it was thought that it is the larva of a member of the Holostomata, closely allied to the genus *Tylodelphis*. The development of another larva, resembling *C. fissicauda*, was followed in tadpoles; this form does not encyst and is said to be a larva of the genus *Tylodelphis*.

A pharyngeal longifurcate distome cercaria, designated *Cercaria A*, was found by Szidat (1924) to develop into *Tetracotyle typica* in *Lymnaea palustris*. Penetration of the snail host takes place very rapidly, usually in fifteen to twenty seconds, and the larvae rapidly make their way directly to the hermaphrodite gland. There a more or less complete structural reorganization takes place, and only relatively late in development is a cyst secreted. The entire development from cercaria to tetracotyle requires from twenty to twenty-five days; earlier workers have shown that *Tetracotyle typica* develops to a species of *Strigea*, probably *S. tarda*.

From this survey of the literature it is clear that much light has recently been thrown on the kinship of furcocercous cercariae to certain groups of adult trematodes. The larvae of the Schistosomatidae, and of some, possibly all, of the Holostomata are included among them. *Sanguinicola inermis* of the Aporocotylidae also has a furcocercous larva.

## INCIDENCE OF INFECTION OF SNAILS

Collections were made through three years, and the method of handling them changed during this time. At first snails were dissected almost immediately after collection, and only furcocercous infections were recorded; percentages therefore include both mature and immature larvae. During the summer of 1921 the method of isolating to secure emerging cercariae was begun; only mature larvae were found, as the negative snails were not later dissected. However, both furcocercous and other forms were recorded. During 1922-23 a complete infection record was kept, including both furcocercous and other infections, emerging larvae and those found by subsequent dissection of the snails.

## MULTIPLE INFECTIONS

As the matter of multiple infections is of some biological interest, the cases found (double infections) are grouped together here.

1. *Planorbis trivolvis* (March 2, 1921) infested with *C. echinocauda* and a redia resembling that of *C. inhabilis*.

2. *Planorbis trivolvis* (March 16, 1921) infested with an unidentified immature furcocercous cercaria and a redia resembling that of *C. inhabilis*.

3. *Physa lordi* (July 8, 1921) infested with an unidentified immature furcocercous larva and the cercaria of *Echinostomum revolutum*?

The third was a single individual given to the author, and so does not appear in the collection records. As all snails were not dissected, it is possible that there were other multiple infections which were not found.

TABLE I

Collection record for 1920-1921; vicinity of Urbana, Illinois.

All snails were crushed; therefore percentages include both mature and immature infections (furcocercous cercariae only).

Species of snail	Place	Date	Number	Infections	Percentages
<i>Planorbis trivolvis</i> .....	C	Oct. 12	53	1 ( <i>C. clephantis</i> )	1.9
<i>Physa gyrina</i> .....	C	Oct. 12	17	0	0
<i>Campelema rufum</i> .....	H	Oct. 30	51	0	0
<i>Planorbis trivolvis</i> .....	D	Oct. 30	7	0	0
<i>Planorbis trivolvis</i> .....	D	Nov. 27	11	0	0
<i>Planorbis trivolvis</i> .....	C	Feb. 16	37	1 ( <i>C. echinocauda</i> )	2.7
<i>Physa gyrina</i> .....	C	Feb. 16	15	0	0
<i>Planorbis trivolvis</i> .....	C	Mar. 2	58	1 (Double infection No. 1)	1.7
<i>Planorbis trivolvis</i> .....	C	Mar. 16	15	1 (Immature Cercaria sp.)	
				1 (Double infection No. 2)	13.3

<i>Physa gyrina</i> .....	C	Mar. 16	10	0	0
<i>Planorbis trivolvis</i> .....	C	Mar. 25	18	1 (Immature Cercaria sp.)	5.5
<i>Physa gyrina</i> .....	C	Mar. 25	1	0	0
<i>Planorbis trivolvis</i> .....	C	Apr. 6	13	1 ( <i>C. wardi</i> )	7.7
<i>Planorbis trivolvis</i> .....	C	Apr. 7	37	2 ( <i>Cercaria</i> sp.)	
				1 ( <i>C. wardi</i> )	8.1
<i>Planorbis trivolvis</i> .....	C	Apr. 19	29	1 ( <i>C. wardi</i> )	3.4
<i>Physa gyrina</i> .....	C	Apr. 19	12	0	0

C, Colvin's Field; D, Drainage Ditch; H, Homer Park.

TABLE II

Collection record, summer of 1921; vicinity of Douglas Lake, Michigan.

Snails were isolated for emerging cercariae and were not later crushed; therefore immature infections were not found.

Species of snail	Place	Date	Number	Infections other than furcocercous	Furco- cercous infections	Furco- cercous percentage
<i>Campeloma</i> sp.....	D	July 4	37	0	0	0
<i>Lymnaea stagnalis</i> .....	S	July 7	30	0	0	0
<i>Lymnaea emarginata</i> .....	H	July 8	28	0	1 ( <i>Cercaria</i> sp.)	3.5
<i>Lymnaea stagnalis</i> .....	H	July 8	8	1 (Stylet)	1 ( <i>C. elvae</i> )	12.5
var. <i>appressa</i>						
<i>Planorbis bicarinata</i>	H	July 8	9	1 (Stylet)	0	0
<i>Campeloma decisum</i> .....	H	July 8	24	0	0	0
<i>Lymnaea stagnalis</i> .....	M	July 8	5	0	0	0
var. <i>perampla</i>						
<i>Lymnaea stagnalis</i> .....	M	July 8	2	0	0	0
var. <i>appressa</i>						
<i>Lymnaea emarginata</i> .....	M	July 8	16	0	0	0
<i>Physa lordi</i> .....	M	July 8	1	0	0	0
<i>Campeloma</i> sp. ....	M	July 8	1	0	0	0
<i>Planorbis trivolvis</i> .....	M	July 8	3	0	0	0
<i>Planorbis trivolvis</i> .....	S	July 20	37	0	1 ( <i>C. elephantis</i> )	2.7
<i>Physa lordi</i> .....	H	July 20	20	0	2 ( <i>Cercaria</i> sp.)	10.0
<i>Lymnaea stagnalis</i> .....	M	July 22	27	0	2 ( <i>C. douthitti</i> )	7.4
var. <i>appressa</i>						
<i>Planorbis bicarinata</i> .....	M	July 22	20	0	0	0
<i>Lymnaea megasoma</i> .....	T	July 24	35	0	0	0
<i>Lymnaea stagnalis</i> .....	B	Aug. 4	23	0	1 ( <i>C. elvae</i> )	4.3
var. <i>appressa</i>						
<i>Physa lordi</i> .....	B	Aug. 4	1	0	0	0
<i>Lymnaea megasoma</i> .....	C	Aug. 9	18	0	1 ( <i>C. chrys-</i> <i>enterica</i> )	5.5
<i>Lymnaea</i> sp.....	C	Aug. 9	3	0	0	0
<i>Planorbis trivolvis</i> .....	C	Aug. 9	73	2 ( <i>Echino-</i> <i>sotome</i> )	2 ( <i>C. tenuis</i> )	2.7
				2 (Stylet)	7 ( <i>C. burri</i> )	9.6
					1 ( <i>C. rhab-</i> <i>docaeca</i> ?)	1.3

B, Bessey Creek; C, Colonial Point, Burt Lake; D, Laboratory Dock; H, Hook Point; M, Maple River; S, Sedge Pond; T, Topinabee Road Pool.

TABLE III

Collection record for 1921-1922; vicinity of Urbana, Illinois.

All snails were isolated for emerging cercariae and subsequently crushed to find immature infections (furcocercous and other).

Species of snail	Place	Date	No.	All infections	Furcocercous Percentage	Other Percentage	Mature Percentage	Immature Percentage	Total Percentage
<i>Physa gyrina</i> .....	D	Sept. 18	97	2 ( <i>C. multcellulata</i> )	2.1	0	2.1	0	2.1
<i>Planorbis trivolvis</i> ..	D	Sept. 18	24	0	0	0	0	0	0
<i>Physa gyrina</i> .....	D	Sept. 28	71	2 ( <i>C. gigas</i> )	2.8	0	2.8	0	2.8
<i>Planorbis trivolvis</i> ..	D	Sept. 28	103	1 ( <i>C. hamata</i> )	1.0	0	1.0	0	1.0
<i>Physa gyrina</i> .....	D	Oct. 21	15	0	0	0	0	0	0
<i>Planorbis trivolvis</i> ..	D	Oct. 21	60	6 (Stylet, mature)					
				5 (Stylet, immature)	0	18.0	10.0	8.0	18.0
<i>Physa gyrina</i> .....	D	Oct. 24	102	2 ( <i>C. gigas</i> )					
				3 (Stylet, mature)					
				4 (Stylet, immature)	2.0	7.0	5.0	4.0	9.0
<i>Planorbis trivolvis</i> ..	D	Oct. 24	31	5 (Stylet, mature)					
				3 (Stylet, immature)	0	25.8	16.1	9.7	25.8
<i>Physa gyrina</i> .....	D	Oct. 26	180	1 (Monostome, mature)					
				2 (Stylet, mature)					
				1 (Stylet, immature)	0	2.2	1.7	0.5	2.2
<i>Planorbis trivolvis</i> ..	D	Oct. 26	101	1 ( <i>C. hamata</i> )					
				14 (Stylet, mature)					
				6 (Stylet, immature)					
				4 ( <i>Cercaria</i> sp. immat.)	1.0	23.8	13.8	10.0	24.8
<i>Physa gyrina</i> .....	S	Oct. 31	23	0	0	0	0	0	0
<i>Planorbis trivolvis</i> ..	M	Nov. 1	9	0	0	0	0	0	0
<i>Physa gyrina</i> .....	C	Nov. 4	81	0	0	0	0	0	0
<i>Physa gyrina</i> .....	D	Nov. 4	177	12 ( <i>C. multcellulata</i> )	6.8	0	6.8	0	6.8
<i>Planorbis trivolvis</i> ..	D	Nov. 4	11	1 ( <i>C. hamata</i> )					
				1 (Stylet, mature)	0.9	0.9	1.8	0	1.8

D, Drainage Ditch; C, Campus Stream; M, Pond at Muncie, Illinois; S, Spoon River, St. Joseph, Illinois.

## Miscellaneous

These snails were isolated for emerging cercariae; they were not subsequently crushed.

*Gonionasis* sp. Olentangy River, Ohio Sept. 1921 200 individuals Negative  
*Gonionasis laqueata* Brown's Creek, Nashville, Tenn. Feb. 1, 1923 378 individuals Negative



## SUMMARY OF RESULTS

1. The furcocercous larval trematode fauna of restricted regions of Illinois and of Michigan has been studied.

2. Seven new species (Miller, 1923) have been here fully described in comparison with morphologically similar cercariae.

3. The literature for one hundred and two fresh-water, and for eight marine species of furcocercous cercariae has been reviewed and summarized; a check list is submitted.

4. Of the new species, the two apharyngeal distomes make clear the establishment of two well-defined groups.

5. The three pharyngeal longifurcate distomes add to the knowledge of this group, in which there are but few complete descriptions.

6. The two longifurcate monostomes, both probably pharyngeal, make possible the formation of a group of these forms.

7. Studies carried on to supplement incomplete descriptions of certain North American larvae have made possible their more exact disposition.

8. It has been possible to make a satisfactory scheme of classification, based largely on the excretory system, for only the apharyngeal brevifurcate distomes.

9. The importance of the excretory system in the determination of relationships is stressed; but due emphasis has also been placed on other features of morphology.

10. From a resume of the literature it is clear that in addition to the Schistosomatidae some members, and probably all, of the Holostomata develop from furcocercous larvae; so also does *Sanguinicola inermis* of the Aporocotylidae.

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## EXPLANATION OF PLATES

Unless otherwise stated, all drawings were made with the camera lucida.  
Abbreviations used:

ao	anterior organ	gb	germ ball
bp	birth-pore	gc	germ cells
c	cecum	hg	head gland
ct	caudal excretory tube	mu	muscle band
d	penetration gland duct	ns	nervous system
da	anterior penetration gland duct	pg	penetration gland cell
dp	posterior penetration gland duct	pa	anterior penetration gland cell
e	esophagus	pp	posterior penetration gland cell
es	pigmented eye-spot	v	ventral sucker

PLATE I

## DESCRIPTION OF PLATE I

All figures concern *Cercaria multicellulata*

- Fig. 1. Diagrammatic view of ventral side, showing probable connections of excretory system.  $\times 760$   
Fig. 2. End of sporocyst, showing birth-pore.  $\times 760$   
Fig. 3. Ventral view.  $\times 310$   
Fig. 4. Diagrammatic outline to show annulations of body.  $\times 365$   
Fig. 5. Ventral view, showing excretory system in relation to other organs.  $\times 760$   
Fig. 6. Transverse section of tail-stem, showing four muscle fields, and caudal excretory tube.  $\times 630$   
Fig. 7. Almost median sagittal section.  $\times 740$

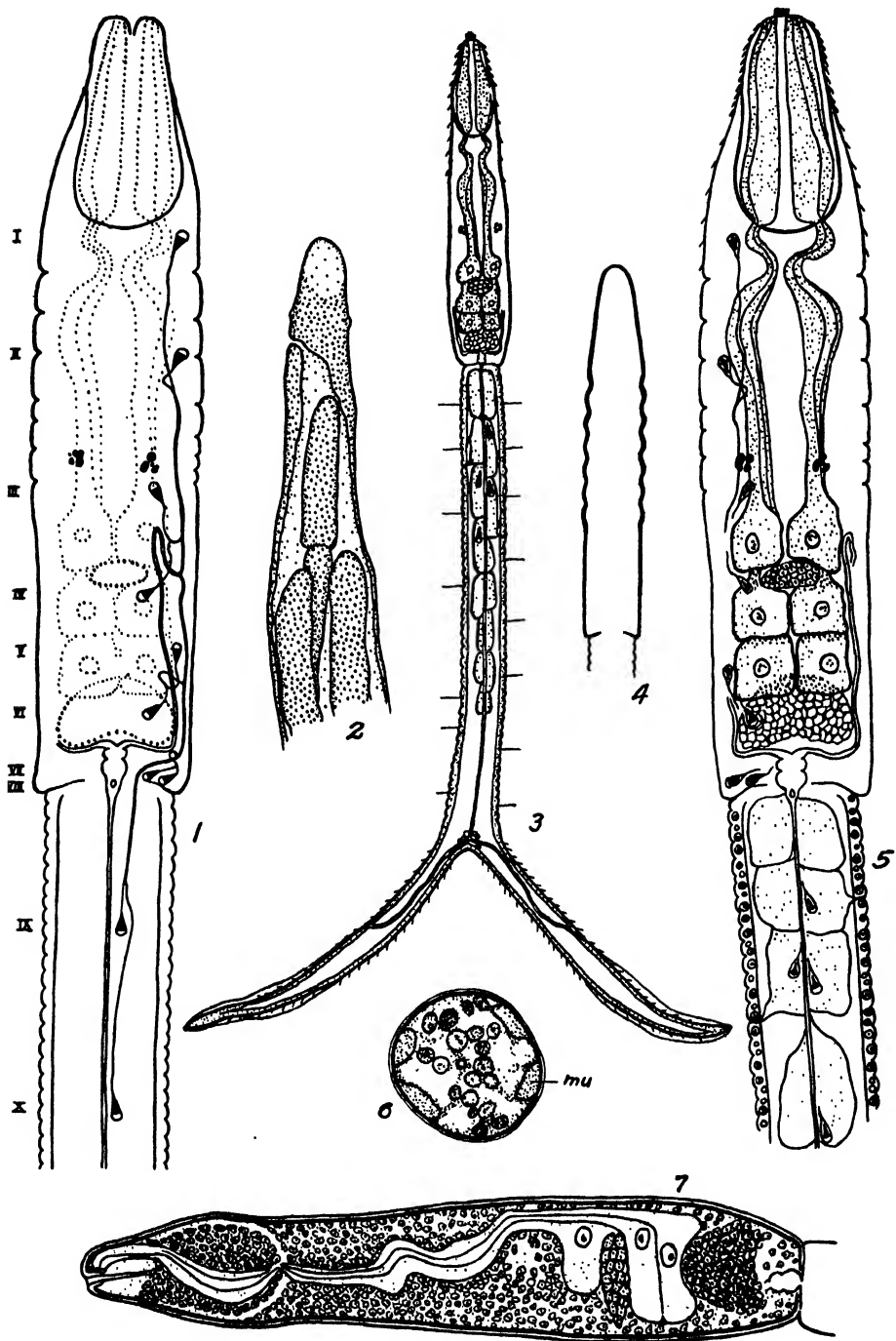




PLATE II



## DESCRIPTION OF PLATE II

Fig. 8. *Cercaria multicellulata*; transverse section through posterior penetration glands.  $\times 740$

Figs. 9 to 16 inclusive concern *Cercaria hamata*

Fig. 9. Transverse section through anterior organ.  $\times 975$

Fig. 10. Transverse section through tail-stem.  $\times 775$

Fig. 11. Outline of living sporocyst containing early germ balls.  $\times 60$

Fig. 12. Semi-diagrammatic ventral view.  $\times 390$

Fig. 13. Outline of club-shaped end of living sporocyst.  $\times 75$

Fig. 14. End of sporocyst showing birth-pore.  $\times 75$

Fig. 15. Transverse section through young sporocyst.  $\times 375$

Fig. 16. Transverse section through anterior germ cell mass.  $\times 1000$

Fig. 17. *C. multicellulata*; transverse section through pigmented eye-spots.  $\times 620$

Fig. 18. *C. multicellulata*; outline of living sporocyst.  $\times 42$

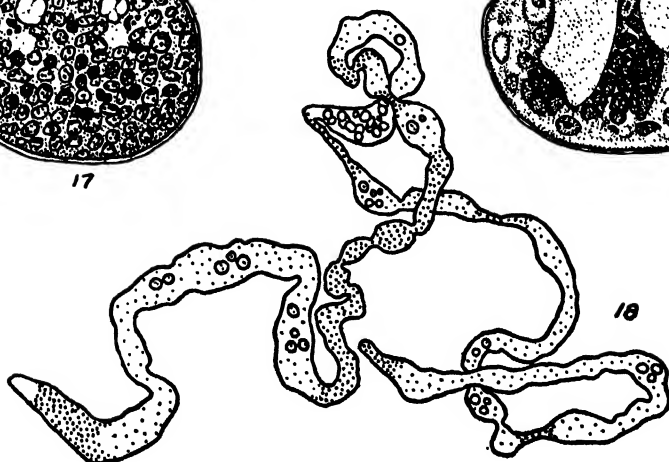
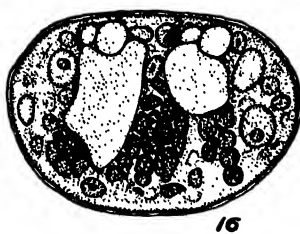
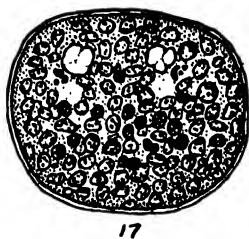
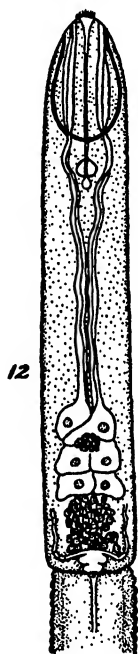
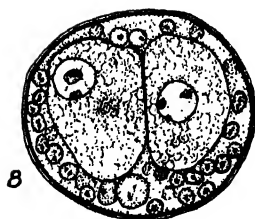
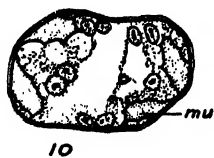




PLATE III

## DESCRIPTION OF PLATE III

All figures concern *Cercaria elvae*

Fig. 19. Dorsal view of body.  $\times 410$

Fig. 20. Ventral view of excretory system.  $\times 410$

Fig. 21. Lateral view of body.  $\times 400$

Fig. 22. Outline of anterior organ, as frequently seen in living animal.  $\times 135$

Fig. 23. Transverse section through tail-stem.  $\times 560$

Fig. 24. Furcal tip, dorsal view.  $\times 115$

Fig. 25. Semi-lateral view of body characteristic of living larva under cover glass.  $\times 155$

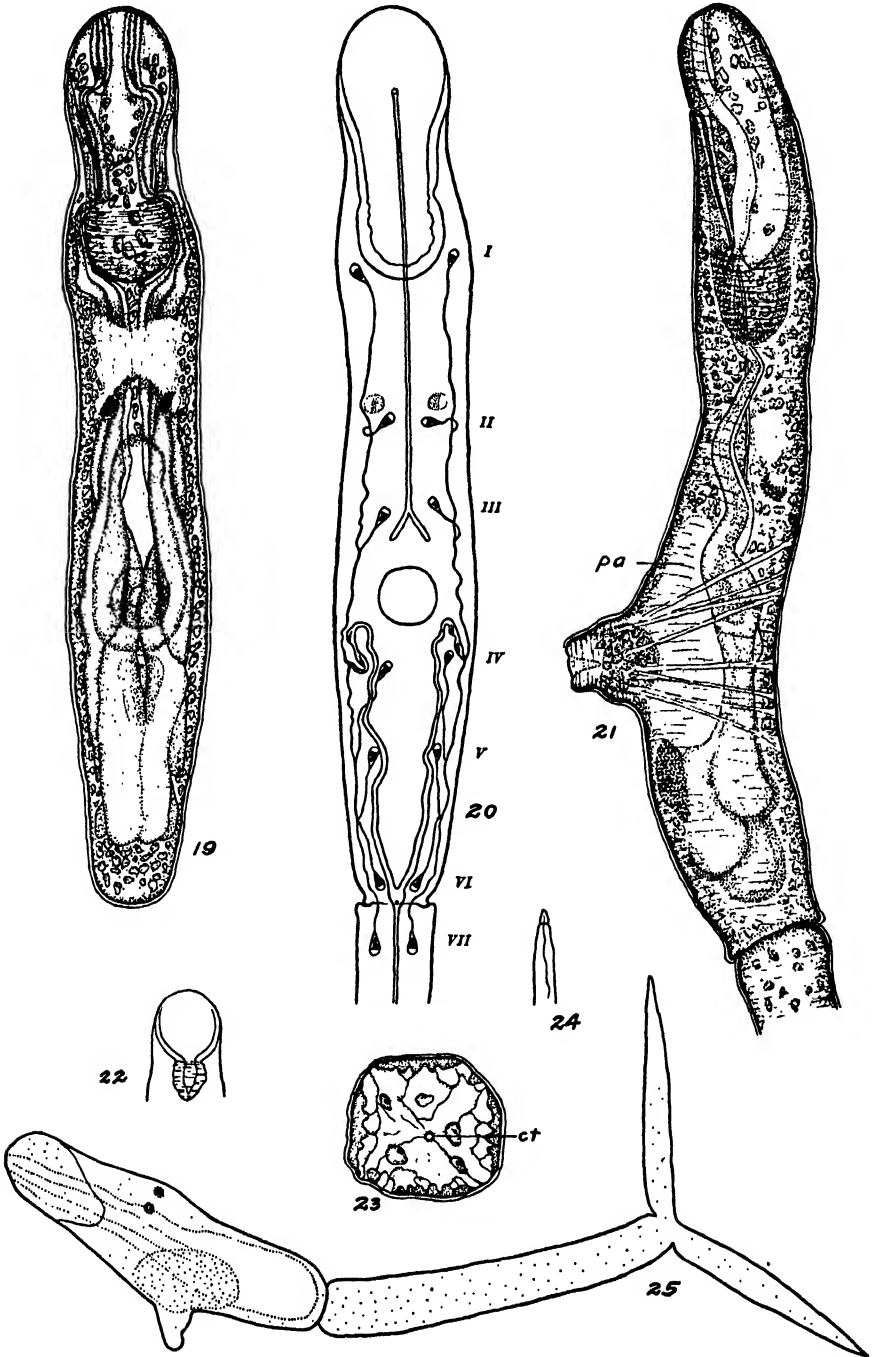




PLATE IV



## DESCRIPTION OF PLATE IV

- Fig. 26. *Cercaria elvae*; transverse section through anterior organ just in front of mouth, showing head gland and penetration gland ducts.  $\times 550$
- Fig. 27. *C. elvae*; transverse section through tip of anterior organ.  $\times 480$
- Fig. 28. *C. elvae*; transverse section through posterior end of anterior organ, showing in addition the esophagus.  $\times 450$
- Fig. 29. *C. wardi*; body outline of living animal frequently observed.  $\times 100$
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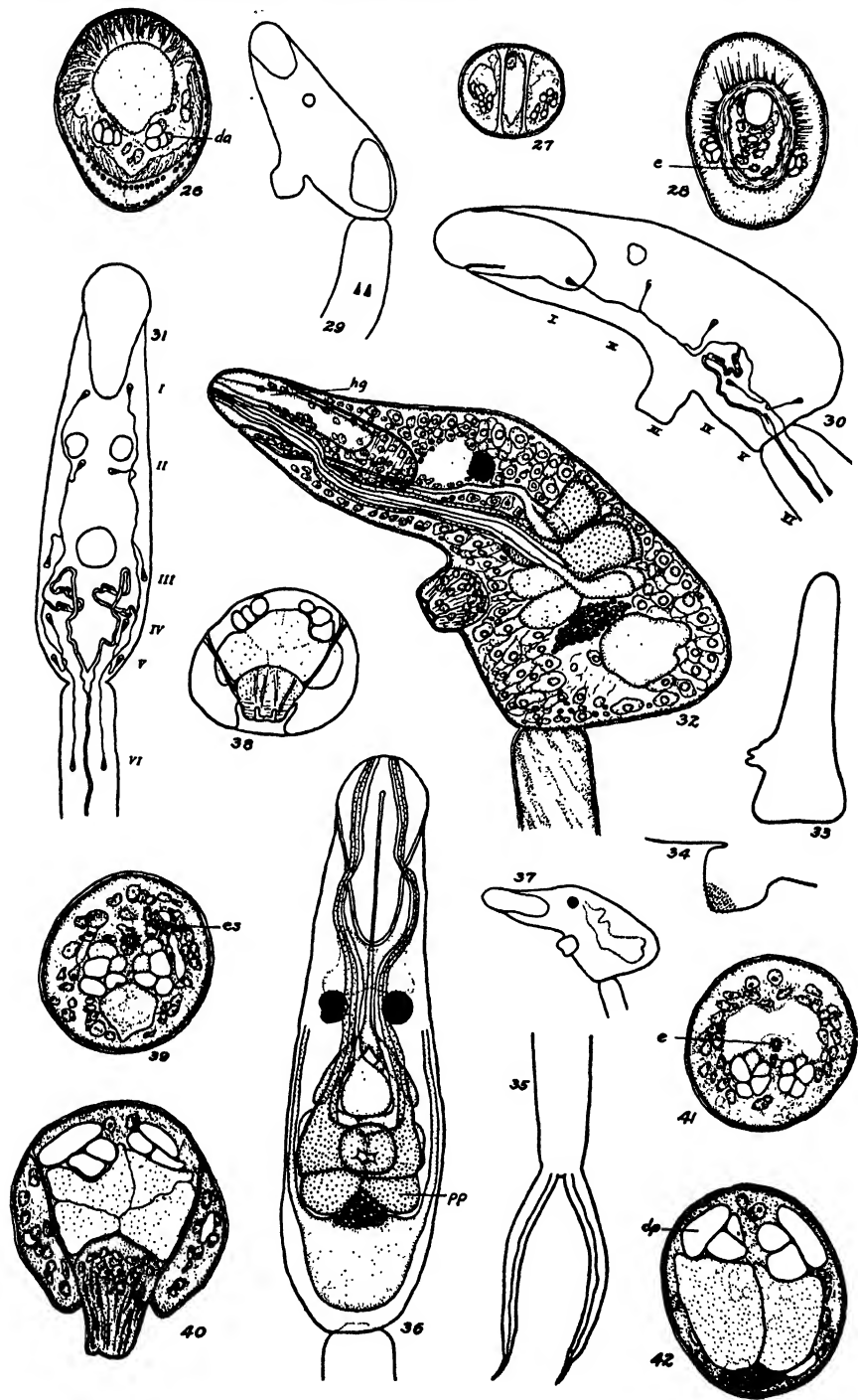




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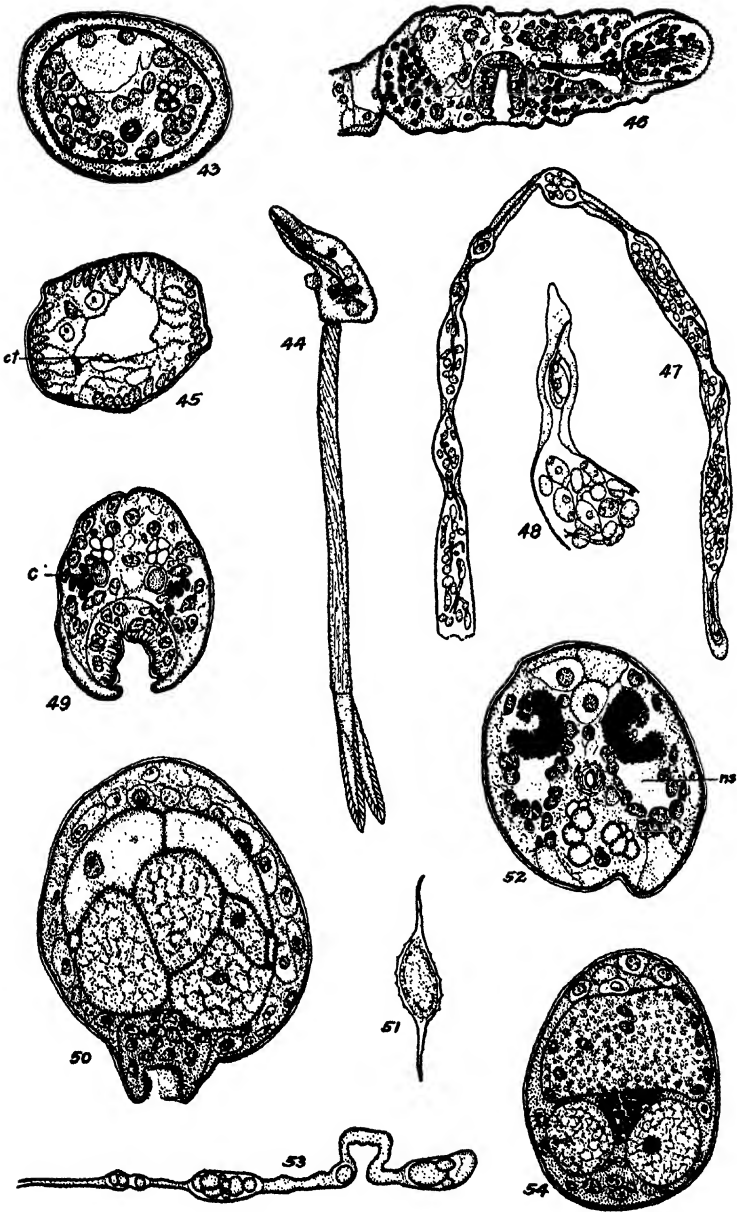




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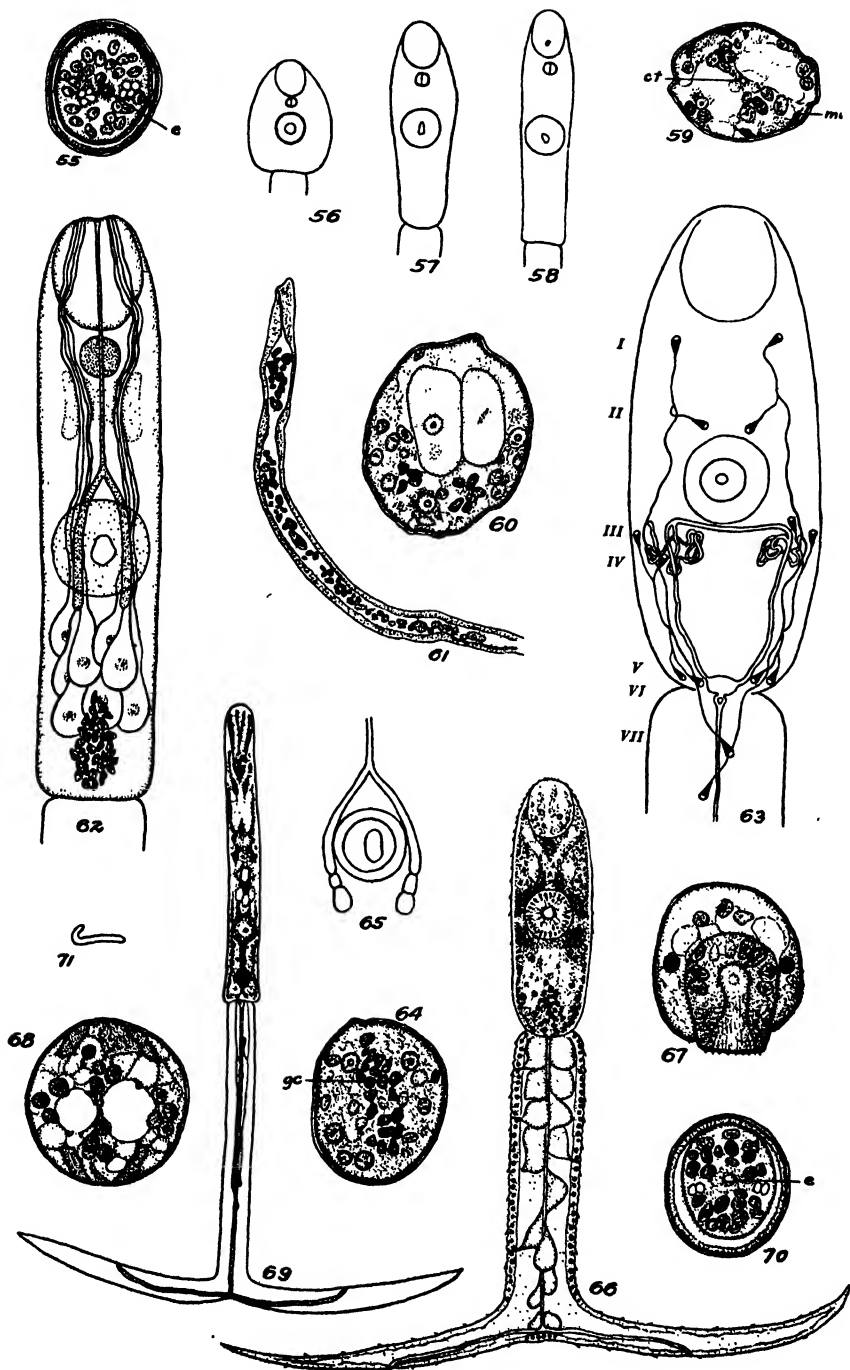




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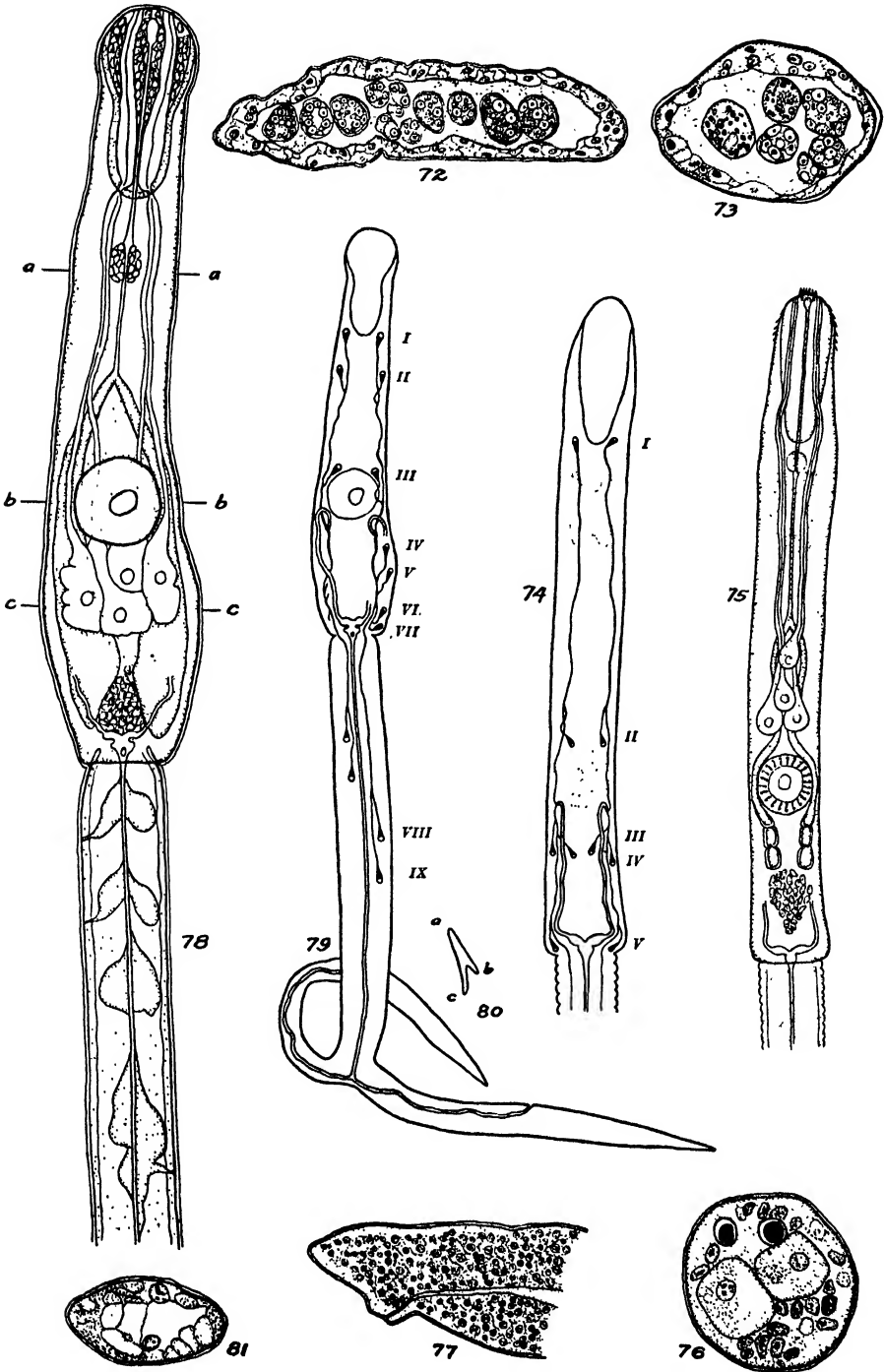




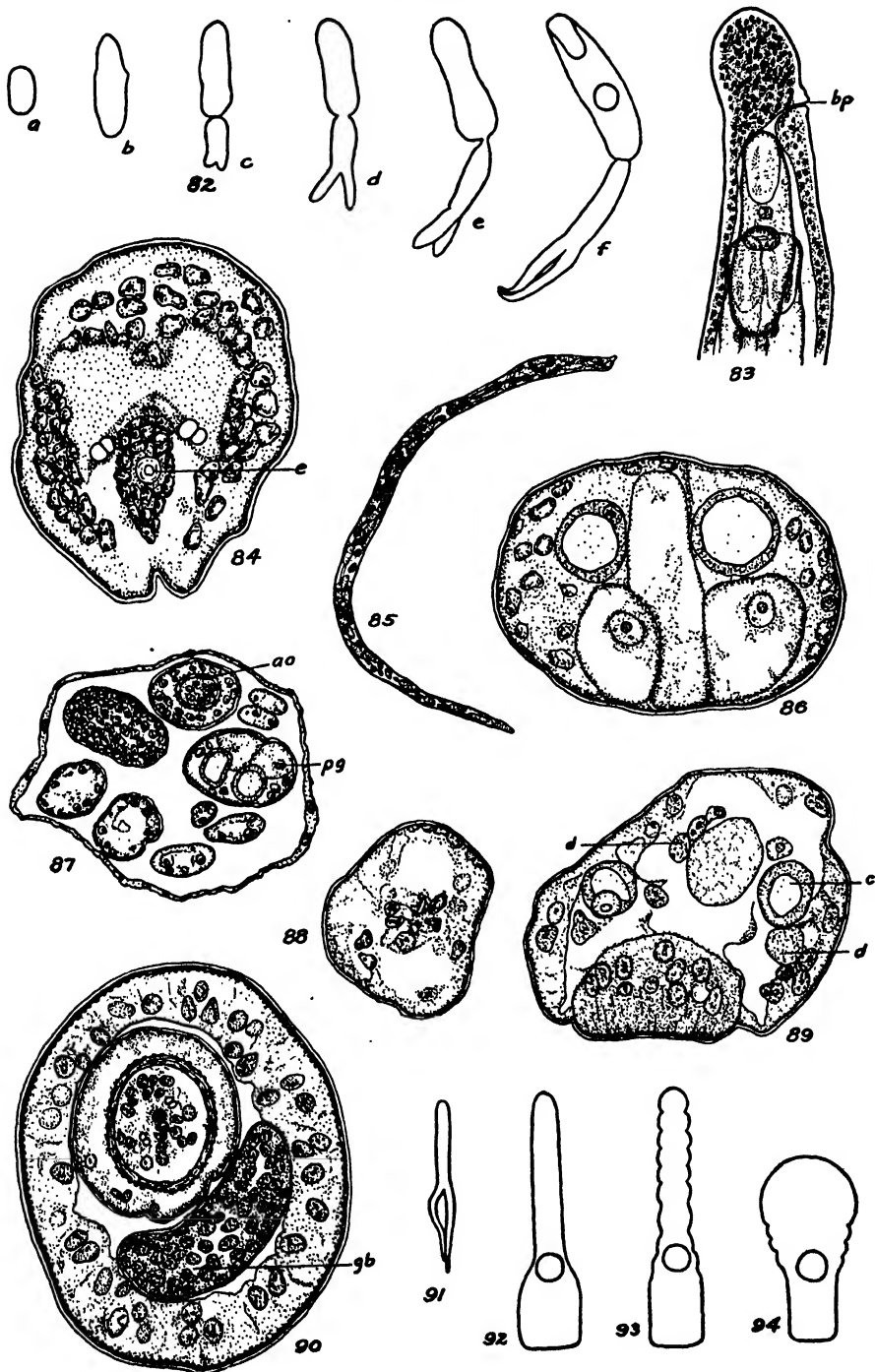
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# A COMPARISON OF THE ANIMAL COMMUNITIES OF CONIFEROUS AND DECIDUOUS FORESTS

WITH 16 PLATES AND 25 TABLES

BY

IRVING HILL BLAKE



**THESIS**

**SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE  
GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS**

**1925**

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## INTRODUCTION

The amount of detailed study given in the past to the community ecology (synecology) of land animals has been much less than that devoted to the ecology of particular species (autecology), a much older branch of the subject. One of the earlier studies in community ecology, from a modern aspect, was that of Davenport (1903), who studied the animal communities of a salt beach. The animal communities of deciduous forest, throughout developmental stages to the climax, have been described by Shelford (1912, 1913), with particular emphasis on succession, and its climax animal community by Adams (1915). Adams (1906, 1909) has given accounts of the animal ecology of northern coniferous forest, and he and his associates (1920) have published the results of an ecological reconnaissance into coniferous forest of the alpine type. These papers were qualitative rather than quantitative studies.

Perhaps in part as a result of the valuable findings obtained in quantitative studies by various plant ecologists and by marine zoölogists, of whom Petersen (1911) may be cited as an example, more recent papers in synecology of terrestrial animals have shown a tendency towards the quantitative method of attack. This method has been employed by McAtee (1907), Beebe (1916), Wolcott (1918), Sanders and Shelford (1922), and Weese (1924).

The present paper deals with the results of several studies of land animal communities and their habitats, made at different times under different environmental conditions. It is hoped to bring out some of the facts of the physical and biotic environments of the communities discussed, the composition of the communities as such, and their relation to certain ecological problems of succession, stratification and hibernation. The viewpoint, and with it the point of emphasis in investigation, has been different for different portions of the work. In the study of the animal communities of the alpine coniferous forest and its predecessors, for example, the weight of attention fell on the process of succession of animal forms, and its relation to plant succession and response to physiographic and climatic conditions. When working in the coniferous forest of the low country, on the other hand, the interest of the investigation seemed to lie particularly in the problems of stratification, and the quantitative and qualitative distribution of the animal societies, as correlated with the results of instrumental measurements of such factors as temperature,

humidity, evaporation and light. The study of the deciduous forest community was essentially a winter study, and while carried on in the same way and with the same ends as the last, its emphasis fell naturally on hibernation, and the responses of the animal societies of the lower strata to the climatic fluctuations.

The following account of the results of these investigations may be subdivided into three parts: (a) a study of the animal ecology of alpine spruce-fir forest, including the various fell-field and tundra stages of which it is the climax, (Figs. 1, 2, and 3) (b) a summer study made in pine-hemlock forest at low elevation, with special emphasis on stratification, (Fig. 4) and (c) a winter study of the hibernating forest-floor population of elm-maple forest. (Fig. 5).

The question of the ecological nomenclature employed calls for particular discussion. It has been repeatedly insisted by various ecologists that biotic communities are in themselves units, and that at last analysis they should be so treated, both plants and animals being considered in their intrinsic and mutual relationships, as well as in relation to physiographic and climatic factors (Clements, 1920). A nomenclature covering plant communities in their various geographic, local, stratal and seasonal subdivisions has been long in use and often revised. A similar nomenclature for use in animal ecology was employed by Shelford (1925). The work of Weese (1924) employs an adaptation of the phyto-ecological nomenclature of Clements to the animal communities of deciduous forest. More recently the attempt has been made by Shelford and Towler (1925) to develop a nomenclature for biotic communities, based on both the plants and animals, and expressing in itself the taxonomic characteristics, permanence or the reverse, seasonal and stratal aspects, et cetera. In the present paper the writer has attempted to follow this classification of animal communities. It should be understood that the names of minor communities based on animals which were numerous in the author's collections and appeared to be characteristic of the stratal and seasonal communities discussed, are put forward in the most tentative way. Several seasons of quantitative collecting should be done in the various strata of a single habitat, before the various sub-communities can be finally named after definite species, with any assurance that the species used are the characteristic predominants of the sub-communities named.

In this discussion the term predominant will be used for species abundant in the habitat (and hence giving a part of its characteristic aspect) and for species affecting the habitat from any angle. The term is a general one. A dominant species is one whose effect on the general habitat is decisive, controlling its character and hence entire biota.

True dominance appears to be a rare phenomenon among terrestrial animals, and is noted only in the few instances where, as in the case of

the short-grass plains of the western United States, herbaceous vegetation was probably kept in a sub-climax condition by great herds of grazing animals.

In the case of denuded areas, the activities of tiger-beetles, digger wasps and spiders, feeding on insects blown in by wind, washed by waves or carried by the predominant predators, open the soil and add organic matter. A similar activity on the part of alpine invertebrates, especially spiders, was noted during this study. The animals in question inhabited the areas of rocks and bare soil produced by weathering and erosion. The animals do not control the habitat as do forest trees for example, but exercise an influence on both the habitat and the biota and are known as influents.

Of the animals collected in sufficient numbers to be considered an important part of the various communities, most exert a minor influence and are known as subinfluents. They may be defined as species which, because of restricted numbers, restricted stratal or seasonal occurrence or for other reasons, have a less effect on the habitat, or the biota balance of the community. Types of subinfluents noted were phytophagous insects, predaceous insects and spiders, and forest-litter animals such as spring-tails and millipedes, whose massed effects on changing the composition of decaying plant debris are of considerable importance to the habitat.

Of less importance to the habitat as a whole is a species that is a dominule; such a species is said to be dominant in a microhabitat of restricted size, within the general habitat. Examples noted were groups of phytophagous insects on their scattered host-plants, and groups of scavengers working on decaying organic matter, such as the body of a dead animal. Such dominules tend by their activities to destroy the microhabitat which they dominate (Shelford).

Climax communities (Clements, 1916) which under existing climatic conditions will undergo no further change, have been referred to as associations. Subclimax communities, in process of succession towards the climax, have been called associates. Seasonal communities, characteristic of different periods of the year, are spoken of as seasonal, and stratal communities, occupying different levels of the same habitat, as stratal societies or societies, depending on their permanence.

## THE ANIMAL ECOLOGY OF THE UPPER SLOPES OF MOUNT KTAADN

### SCOPE OF WORK

The work on which this study is based was done during a reconnaissance made in the summer of 1923. A base was established at an elevation of 2,400 feet on Basin Pond, and another higher up at Chimney Pond, at an elevation of 2,900 feet. An outlying camp was maintained from time to time on the so-called Saddle, at an elevation of 4,275 feet. From these points the various stations were visited and studied, collecting being done at typical places. With the exception of a single maximum and minimum thermometer, instruments for the study of the environment were not available. In compiling the lists of animals for the various stations, certain species have been added from the literature and from information gained in correspondence, particularly in the case of vertebrates; the sources of this information have been given in all cases. Much more data could be gleaned from the published taxonomic lists, if the local habitats were given; as this is frequently not done, many species listed as occurring on Mt. Ktaadn are not included, since it was impossible to place them in the scheme of classification by habitats which was a part of the plan of study. Exceptions to this have been made in the cases of species where the combination of elevation and restricted food habits of the animal make it possible, in the absence of other data, to assign it with some confidence to a given habitat. Where the habitat was known, or could be with reasonable certainty inferred, it seemed advisable, considering the general inaccessibility of the area and the small amount of zoological work that has been done there, to include what published records were available in the present lists. On the other hand, of the many species collected and determined, only such are considered here as approach, either *numerically* or otherwise, the status of predominants.\*

In considering the local environments of the various animal communities, it has seemed wise to include rather full accounts of the plants found, taken in part from lists made in the field and in part from published work of various botanists. This is done in general to give as detailed an idea as possible of the animal habitats, and particularly to facilitate further studies of food relations of various phytophagous species to their environment.

\*Dominants of Clements (1920) and Weese (1924).

In general it may be said that the principal aim in this part of the investigation was to trace the process of animal succession from bare rock to forest, gaining what light was possible on its factors and causes.

#### THE ENVIRONMENT

The special ecological significance of Ktaadn is due primarily to its height. This is great enough—in a low and generally flat country—to have made its upper slopes a refuge for alpine species when, at the retreat of the last ice sheet, they were marooned by returning warm conditions (Adams, 1905). On the plant side it is quite obvious, even from a casual glance at the vegetation, that these arctic, or at least alpine species are being invaded by more mesophytic forms that are gradually spreading upward, in the face of severe handicaps of montane soil and climate. The persistence of their advance hints at eventual extinction of the less adaptable and less abundantly growing natives of the Arctic fell-fields. What is true of the plants will be seen to be equally true, even if less immediately obvious, of the animals of these upper regions of the mountain.

The general topography of Mount Ktaadn and its relation to the surrounding country have been so often and so well described (Hamlin, 1881; Tarr, 1900), that the writer will attempt no more than such a sketch as will render comprehensible the location and physiography of the areas studied. The location of the mountain is the north central part of Maine, between the eastern and western branches of the Penobscot river. It is stated by Harvey (1903a) to be 1°, 37', 15", or about 112 miles, north of Mount Washington, the highest point in New England, and is itself the second highest point. The general conformation is that of a long, table-topped mountain, rising rather abruptly from the surrounding country, and much less subdued, especially on the eastern face, than is the case with many other mountains of the northeastern United States. There are a number of special features other than height that should be considered from the standpoint of a biotic environment.

First of these to be mentioned is area. Ktaadn is remarkable for the large extent of its upper regions, the entire mountain being about nine miles long and of varying width, the whole covering a very considerable area of alpine biota. The central plateau covers more than five hundred acres (Hamlin, 1881) and smaller areas of greater elevation on the south and larger areas in the vicinity of the northern peaks, increase to very respectable proportions the total alpine areas. Such opportunities for the study of mountain life over a considerable extent of territory are rare among eastern mountains, and for this reason Ktaadn presents to the ecologist some advantages over mountains that are its superiors in height. The equal exposure of the mountain to weather conditions on all sides, a fact caused by the isolation mentioned below, is another factor of some



importance in considering the habitat relations. Thus the effect of prevailing winds and other climatic factors on the mountain life show themselves very plainly, uninfluenced by protection from neighboring heights. Another special feature, which will be seen to be important in the consideration of the environment of various communities, is that of drainage. The precipitation, as will be seen when the climatic factors are taken up in detail, is decidedly heavy as compared with that of coniferous forest at lower levels. But the rapid run-off on the steep slopes and the seepage of water from the scanty soil down among the underlying boulders on the level areas, combine with the high evaporating power of the air to rapidly remove the effects of the abundant rainfall.

Certain features of the local topography are also of importance in determining the distribution of the various biotic associates.

Portions of the walls of the glacial cirques, especially prominent on the eastern side of the mountain, are so steep as to support no life, being washed by water and scoured by the detritus of erosion of higher regions. If, however, there is any opportunity for soil and water retention, even here plant immigrants make good their stand, and at least a visiting animal population occurs. On the long dirt and rock slides conditions are more precarious, for frequent erosion gives plants little opportunity to establish themselves save at the borders of these slides, where conditions are somewhat more stable. Here is a characteristic biota, which seems to be in some respects a combination of types found in the various succession stages on the plateau above. Plant succession on the plateau, which may be considered as typical of the process over most of the mountain, involves (Harvey, 1903a) successive associates of crustaceous lichens, reindeer-Iceland mosses, alpine tundra and krummholz, all leading up to the climax *Picea-Abies* forest of the entire region. This conception served as a general guide to the writer in selecting stations for study, although, as will be seen later, it seemed necessary in considering the animals to combine some of these stations and subdivide others. For the present we may accept the stages as given by Harvey and consider their local distribution.

It is customary to consider the distribution of mountain biota as showing at least rough zonation with reference to altitude. This condition occurs on mountains sufficiently high to afford a true climatic timberline. Ktaadn, however, appears not to be high enough to possess such altitudinal zonation, and the local distribution of the various plants and animals is determined by other factors than those of altitude. For this reason we look in vain for any set altitudinal order of the various stages of succession, even under identical conditions of slope exposure. Just below the summit occur small mats of the climax trees, though dwarfed and prostrate from edaphic conditions and exposure to strong and continuous winds. On

the other hand, there are wide treeless areas at altitudes far below those of considerable growths of stunted but thickly-growing spruce and fir. In a similar way the earlier stages of plant succession, involving various steps from rock through alpine tundras to krummholz, appear wholly determined by physiographic and edaphic conditions, indubitably earlier stages occurring many hundreds of feet below older ones. This explanation is made in order that it may be understood why the various plant and animal associates are scattered in groups of various sizes very irregularly, and not necessarily correlated with altitude. Thus it will be seen that stations consisting of extensive areas of primitively bare rock may exist, as the one chosen for study did exist, considerably below the altitude where occurred a well established mat of alpine grasses and sedges, representing the second stage of tundra succession.

The *general topography* of the mountain has already been discussed, particularly in its relations to biotic communities. Ktaadn is characterized among eastern mountains by its isolation, rising from the heavily wooded lower lands, with no serious rivals in its vicinity. Its gradual lower slopes rise, in most places to nearly three thousand feet, before terminating somewhat abruptly at the steep ascent to the tableland and upper slopes. This upper region, which constitutes the mountain proper, has been described (Harvey, 1903-a) as a "long, narrow, fish-hook shaped, serrated crest, bristling with peaks and divided by the low central mountain, the 'saddle', into the North and South Mountains from which jut out spurs in all directions, enclosing several well-defined basins." The highest, or West Peak, is in the southern group, with an elevation of 5,273 feet.

The mountain is composed of granite, the lower portions being gray in color and hard, the upper red, and readily weathering to form at first a coarse, and later a finer, granitic soil. The character of the soil in the local areas studied will be taken up in more detail later.

There have been no climatic studies made on Ktaadn, and little has been done in this regard on any of the New England mountains. The United States Weather Bureau maintained a station on Mount Washington (about 160 miles south and west of Mount Ktaadn) at an elevation of 6,293 feet, during the summer months of 1859, through the years 1871-1886 inclusive, and intermittently thereafter, mostly during the summer months, until 1892. Most of the data taken has been published, and some unpublished data have been kindly communicated by the Bureau. The University of Vermont maintained an observation station on Mount Mansfield (4,075 feet) during the summer of 1919, during which temperature, humidity, evaporation, wind velocity and sunshine were recorded. A short study was made on Mount Marcy (5,344) by Adams and his associates (1920), embracing temperatures, evaporation and solar radiation; this included only a period of five days.

The writer had at Ktaadn a maximum and minimum thermometer, whose reading had been corrected by a standard instrument. This was exposed in the shade of spruce-fir forest at Basin Pond (2,400 feet) from June 12 to July 29, with one break between July 23 and July 27. The station was that selected as the lower of two representing climax conditions (Station E). The results of these readings, a maximum and minimum for each twenty-four hour period, are shown as a graph (Fig. 8). It will be seen that the daily variations are considerable, and more marked, on the whole, for the maxima than for the minima. Even in the case of a shaded thermometer, the daily ranges are seen to be:

Maximum	17.5°C
Minimum	2.5°C
Mean	9.0°C

The temperature ranges between different strata, and between open and shaded areas, while not measured, must have been marked.

From July 30 until August 18, with occasional interruptions due to absences on side trips, the same instrument was read twice daily in similar habitat at Chimney Pond, 500 feet higher (Station E-2). This point lies in the great South Basin, at the foot of the steep ascent to the highest peak, and has generally been considered as a region of climatic stress. It did not seem remarkable, therefore, that the daily ranges should be somewhat greater:

Maximum	19.0°C
Minimum	3.1°C
Mean	11.0°C

Since these readings were taken during the latter part of the study, when the temperatures were gradually falling, as is indicated by the graph (Fig. 7), the comparison of the actual temperatures, as contrasted with the ranges, with those taken earlier at the lower station, cannot be of value. The entire data indicate a low summer mean temperature, varied by considerable extremes in both directions.

On Mount Washington, the mean monthly temperatures as observed by the United States Weather Bureau for the years 1873 to 1886 inclusive, are as follows, expressed in °C:

January	-17.8	July	8.9
February	-16.2	August	7.6
March	-14.5	September	3.4
April <sup>o</sup>	-6.8	October	-1.8
May	-.3	November	-9.7
June	6.5	December	-15.4

It will be seen from these figures that the temperature conditions expressed are relatively severe. The mean maximum temperature over the same period of years was  $9.2^{\circ}\text{C}$  the mean minimum temperature  $-20.8^{\circ}\text{C}$ . The monthly mean minima are always below the freezing point. A portion of this data has been plotted as a hythergraph (Fig. 9), which will be discussed later. At present it may be pointed out that the mean monthly temperatures are distinctly lower, and the climate corresponding more severe, than that of Orono, lying considerably farther north, but with an elevation of only 129 feet.

There are no instrumental studies of precipitation for Mount Ktaadn. The records from Mount Washington, however, are significant, and are in decided agreement with what has been observed and reported—but never actually measured—for Mount Ktaadn. Both mountains lie sufficiently near the sea to be, in general, subject to a maritime climate as distinguished from a continental one, modified by such factors as their altitude may serve to produce. The effect of this on precipitation is greatly augmented, as the upper slopes are sufficiently high to “intercept moisture-laden clouds and precipitation is almost daily and frequently excessive” (Harvey, 1903-a). On about half the days of the writer’s visit, there was more or less rain, either on the upper slopes or over the entire mountain. This was frequently of many days duration, and sometimes almost torrential in character. The mountain has always had a popular reputation for heavy precipitation. Judging from the recorded conditions on Mount Washington, as well as from the observations of various persons on Mount Ktaadn, the weight of precipitation must fall as rain during the warmer season. But the reports of lumbermen who worked from Basin Pond (2,400 feet elevation) for several winters, indicate the presence of a heavy winter snowfall. In general it may be said that abundant precipitation occurs, and the xerophytic aspects of some of the plant communities are due to other factors, such as rapid run-off and high evaporating power of air. The hythergraph (Fig. 9) gives the condition on Mount Washington. It will be seen that there is a large precipitation, well distributed, and falling more in the warmer portion of the year.

The only study of evaporation on northeastern mountains, so far published is the short study of Adams (1920) on Mount Marcy, already referred to. Here there was a correlation between increased altitude and increased evaporating power of air, apparently modified for certain stations by the character of the plant cover and the amount of available moisture in the substratum. But even without measurements, it is evident that evaporation on the upper slopes is very great. The wind velocity, referred to below, coupled with the presence of only a thin soil and scanty plant cover, especially in the upper stations, makes for a high degree of water loss. In spite of the abundant rainfall, little or no standing water is found

in depressions of the rocks, except as these are of considerable size. The ground and alpine mat are soon dried on the surface after even the heaviest rain; the great evaporating power of the air thus offsets some of the effects of the large precipitation.

The scanty data on air movement, aside from general observations not made with instruments, come from Mount Washington, where the average velocity over a period of twelve years was 105 miles per hour. The velocities of wind on Mount Ktaadn are apparently of the same order, although there have been no measurements taken with instruments. It is a matter of common observation that very strong winds are the rule, and the vegetation shows the same modifications of growth-form (Harvey, 1903-a) that have been described for the plants of the higher mountain. This high rate of wind velocity has been noted in connection with evaporation, and it no doubt increases the stress of the other climatic factors, such as temperature and precipitation extremes, in the effect on the biota.

Studies on light are wanting, the nearest approach being the solar radiation studies carried on on Mount Marcy by Adams, with the aid of black and white spherical atmometers. These showed a general increase of light as the upper stations were approached, correlated with the decreasing plant cover.

In an attempt to get some idea of the conditions of the soils of the upper slopes, with particular reference to plant and animal succession through the various habitats, a number of soil samples were collected from various stations and later submitted to chemical and physical analyses. The results are given in Table I. Two important soil factors, temperature and hydrogen-ion concentration, were not investigated for lack of proper equipment. The results are of some interest, as showing certain apparent differences between tundra and early forest soils, in montane conditions. It will be seen that of the dry matter (the proportion of water not being considered as significant because of the time that elapsed before the analyses could be made) the greatest percent of inorganic material occurs in the sample taken from early (grass) alpine tundra at station C (Fig. 1), while the difference in this regard between the late (heath) alpine tundra at station C-2 and the early forest (krummholz) stage at Station D (Fig. 2) do not seem significant. Correlated with this is the fact that the first of the three soils named possesses the lowest organic content (39.6 parts per hundred) while the difference between the amounts of organic matter in the heath tundra and krummholz (respectively 75.5 and 74.1 parts per hundred) is insignificant. It might appear from this that the qualitative changes from a purely mineral to a partially organic soil have taken place during the gradual transformation of grass to heath tundra, and that by the time the latter is reached the soil if deep enough is able to support the krummholz, as far as wind, moisture and other climatic conditions permit it to become established.

The nitrogen relations are less simple, and perhaps averages of further samples would alter them. They indicate a higher percentage of nitrogen for the late than for the early tundra, but a surprisingly low nitrogen percent for the krummholz soil. Adams (1920) found a somewhat higher nitrogen value for the krummholz as compared with the tundra soil, as would naturally be expected. The acidity figure, given by titration with  $n/100$   $\text{Ba}(\text{OH})_2$ , is highest for the krummholz soil; the relatively low acidity of the soil from heath tundra, as contrasted with that from grass tundra, is difficult to account for. It is likely that the investigation of the specific acidity of these soils by the methods of color indicators would yield more illuminating results.

The primary soil formed by erosion of rock is at first a purely mineral one. With the process of biotic succession, the remains of organisms, beginning with the remains of the pioneer plants and animals, add more and more organic material. This is indicated by the increase of organic matter and corresponding decrease in purely mineral material, noted in the comparison of soils from early and late tundra stages. It is an ecological truism that this process is accompanied by the process of plant succession. The details of the accompanying animal succession, as observed in the alpine communities under consideration, will be considered.

#### THE BIOTA

The peaks and upper surfaces of Ktaadn display large rock areas, tundra-like stretches, and compact islands of krummholz. It is over these areas that the process of succession was studied. Before, however, going into the details of the various stations, and the plants and the animals found there, it will be necessary to say something of the animals of this upper region as a whole, and especially of the vertebrates, which from their larger size, better powers of locomotion, and superior powers of adaptation, show a more general distribution over the upper slopes, and less restriction to the minor succession stages than the invertebrates. In fact, with a very few exceptions which will be spoken of in due course, it might be said that the vertebrates of Ktaadn present two, and only two, great communities, and that even between these two there is considerable overlapping of particular species, or rather, that one community, the climax, possesses a total vertebrate population inclusive of all or nearly all the species of the entire area, while the other, subclimax area is inhabited by a vertebrate population composed of certain species of the climax animals, while others do not appear in these early associates. It will be seen from a comparison of the tables (Tables II, III, IV, V and VI) that the number of vertebrate species appearing in the subclimax stages, but absent from the climax, is extremely small; indeed, perhaps a more extended investigation of the climax would show that there were none. These two commu-

nities are those of the heavily wooded belt of coniferous forest from which the steep-walled upper slopes abruptly rise and the alpine plateau itself.

It is not to be understood that any distinction can be drawn, separating the animals of one taxonomic group ecologically from those of other groups inhabiting the same area; we cannot speak of "vertebrate associations." On the contrary the community, as a biotic unit, must be considered as made up not only of all the animals but of all the plants of a habitat, and even these organisms present important relations with the physical environment, as well as with each other. But when it happens, as in the present case, that a group of animals ranges indifferently over a series of associates, to the individual stages of which certain other animals are more closely confined, it would seem to make for brevity and even for unity to discuss them as a unit in their relations to the entire diversified series of habitats over which they range. This is in agreement with the usage of plant ecologists (Clements, 1916), who consider that a formation, such as the coniferous forest (climax) which we are considering, is composed not only of the areas dominated by climax species but also of areas dominated by subclimax species; in this sense, the subclimax rock, tundra and krummholz stages are a part of the formation. It is interesting to see that the larger animals of the tundra are almost identical with those of the climax forest. It suggests that the larger animals, especially but not wholly vertebrates, use the subclimax area as a part of the formation, in accordance with the conception stated above. A similar condition has been suggested (Shelford, 1913) for the relations of some of the larger animals, especially mammals, to the various subclimax stages of deciduous forest.

So far as known, amphibians and reptiles do not occur on the upper slopes. The long distance from suitable breeding-places is probably the reason for the absence of the former, which, as will be seen, are fairly abundant in various places lower down.

Small birds appear not to frequent such unprotected places as the plateau of Ktaadn, despite the fact that there is abundant food in the form of numerous insects and fruits of the thick-growing ericads, especially blueberries and cranberries, but also *Cornus canaednsis*, bearberry, and other fruits. Comparing the tables (Table IV, V) the marked absence of small passeriform birds will be very evident. Two forms, the junco and the white-throated sparrow, do occur, but they are exceptions among a much larger number of small birds that stay behind in the lower forest. Of the few birds listed, a large proportion are raptorial. The goodly population of small mammals of the upper regions, coupled with the fact that they are perhaps more easily seen and captured on the open tundra than in the thick lower forest, may account for this. Besides, these birds are powerful in flight and able to maintain themselves in the constant high winds as the smaller species are unable to do. They hunt over the lower

forest, however, as well. The grouse is probably a visitor, coming to feed on the abundant fruits of the heath plants.

Considering the mammals of the mountain (Tables II, III) we find that a larger number of species is listed from the tundra and krummholz than is listed solely from the climax forest. Of course, it should not be overlooked that the list is actually much smaller for the tundra, since all the forms found there, or almost all, are found also in the spruce-fir forest. But if we should strike out from Table III the species which are largely associated with the local, waterside communities, such as pond- and streamside animals, we see that the proportion of forest-dwelling mammals that range more or less freely out onto the tundra is even larger than that suggested by the lists as they stand.

Adams (1920), in speaking of Mount Marcy, says "No evidence of permanent residents among vertebrate life were found by us in the alpine area." He quotes Batchelder (1896 and correspondence) however, on the presence of several species of mice and shrews.

Of the mammals listed for the upper stations of Mount Ktaadn, three, the white-footed mouse, the red-backed mouse and the short-tailed shrew, live as summer residents, at least, on the open tundra among the piled rocks and alpine turf. The red squirrel is a frequent visitor in these areas, but his true alpine home is among the krummholz, as might be expected, and the same is no doubt true to a less extent for the porcupine, which appears to den indifferently, in summer at least, "in the fir scrub and rock heaps" (Dutcher, 1903). The varying hare appears more abundant, to judge from the "sign," in the krummholz, but it too appears to occupy the tundra to some extent, since Dutcher took it "on the tableland." He gives the masked shrew only as a krummholz animal, whereas from the report of Batchelder it probably could be found by extensive search on the tundra.

The case of the bog-lemming is of some interest. Dutcher, in 1902, found the whole mountain top showing abundant old microtine sign, but was able in extended trapping to take only two specimens, which were taken from the krummholz. In 1923, the writer found the evidences of a large colony of microtines on the grassy tundra of the tableland, just below the summit, consisting of characteristic holes, run-ways and grass-cuttings. Extensive trapping failed to take a single specimen here or in other localities, and the work appeared to be old and disused, but probably, from its appearance, had been occupied at least during the preceding summer. Two other points are of significance in this connection. Dutcher, in two months trapping with about ninety traps, covering all the typical areas of the mountain, took only nine specimens of the white-footed mouse, and states that they are not abundant. On the other hand, he does not mention the red-backed mouse as occurring on the upper slopes at all. The writer found, in 1923, that these last two animals were



very abundant at all levels, and especially at the upper stations. These facts are suggestive, if no more, in the light of work that has been done in this country and abroad on cyclic fluctuation in the numbers of mice and other animals in a given locality (Elton, 1924; Howell, 1923; Seton, 1920). These authors suggest a periodical fluctuation in numbers of many animals, to be explained, in part at least, by cyclic climatic changes, and for some species of mice a 10-11 years cycle has been proven (Elton). Nothing is known of the climatic conditions on Ktaadn or the other New England mountains during the years 1902-1923 inclusive; but the markedly different findings of Dutcher and the author, using the same methods of study on two species occupying the same area, suggest a similar rhythm of increase and decrease for these two species. It is known that several species in a given area may thus increase and decrease together, or within a year of each other. These things suggest also the value of observation being carried on in alpine areas through a series of years, if this could be done for a single locality.

The carnivores of the upper stations of Ktaadn are three in number, as reported. Nothing is known of their abundance there, although the guides report the foxes fairly common in winter, while the lynx has been reported as a winter visitor. The small brown weasel was taken by Dutcher in the krummholz, but since he says it is abundant at all altitudes, it must be found also in the upper tundra regions where it would find a rich prey among the teeming rodent population. The larger carnivores, especially in winter, probably feed extensively on the varying hare.

The most interesting animal of the Ktaadn tundra, now no longer found there, was the woodland caribou. Up to about twenty-five years ago, the winter feeding grounds of these animals were the tundra areas whose mosses and ericads, cleared of snow by the winds, furnished an abundant pasturage. About that time the herds were slaughtered or driven off, and the survivors no longer visit the mountain or indeed the state. Harvey says that the caribou herds came "from the north" and Dutcher that there had been "two migrations of caribou from Northern Maine," the last within six years of his visit. On the other hand, Mr. Dudley told the writer that the migration to and from the mountain was annual, the animals passing the summer in the bog-forest which covers so much of the adjoining area, and is interrupted by more open boggy areas. No doubt the first two statements apply to general migrations by which at varying intervals the numbers of these animals were increased in the whole region, while the last refers to local seasonal migrations. Ecologically the caribou is of interest as a typical tundra animal which, living in the forest, has as far as possible maintained its tundra habits, clinging to the scanty areas of low and high tundra that break the great expanse of ever-green woods.

Considering the tundra vertebrates as a group, both in their biotic and physical environmental conditions, we may say that with one important exception, the caribou, they are a group of coniferous forest animals which have made themselves at home in the earlier successional stages of that habitat. For certain of the lower forms this was impossible, either because of breeding habits restricted to water or for other reasons; thus we find no amphibians nor (s. f. a. k.) reptiles in the upper regions. For animals that can bear the more stressful climatic conditions of the upper areas, the higher stations furnish a region of abundant food supply, probably more so than is found in the forest itself, considered as a whole. For certain types of animals, especially those that can take refuge in rocks and stunted scrub, the tundra or krummholz or both furnish entirely adequate shelter and materials for abode. Thus we find a very large percentage of the woods mammals, especially the smaller species, habitually occupying the tundra and krummholz stages as well. A considerable number live entirely on the tundra; to this group belong the white-footed mouse, short-tailed shrew, red-backed mouse and probably masked shrew and weasel. Another group makes its abode in the krummholz and feeds on the tundra; here belong the red squirrel and varying hare, and perhaps the porcupine. Still a third group, while making its headquarters in the spruce-fir forest, are temporary residents of krummholz and tundra; these are the red fox and Canada lynx, and perhaps the woodchuck, concerning whose occurrence at the upper stations, however, little is known. The caribou and probably the bog-lemming are, on the other hand, true tundra animals.

If we now compare the number of forest birds found in the upper stations with the number of forest mammals found there, we see at once that the proportion is much smaller, and only a very few of the smaller species are found, of which the hardy junco may be named. As far as at present reported, about one-half of the forest species occurring also on the tundra are strong-winged raptorial forms, and if we omit the somewhat doubtful occurrence of the ruffed grouse in considerable numbers, more than half. The relative absence of small birds as compared with small mammals is particularly striking. The food supply, as has already been suggested and as will be seen more clearly when the invertebrates and plants are considered in detail, is probably more abundant on the tundra and equally abundant in the krummholz, as in the climax itself. The materials for abode, the importance of which was suggested by Shelford (1913), must be equally well supplied by the krummholz. There is no reason to consider enemies more abundant; indeed there is some evidence, based on various carnivores which do not reach the upper stations, that they are less so.

Shelford (1914) has shown that among stream animals the communities may be divided on the basis of extent and nature of response to varying strengths of current, which is the dominant physical factor in that habitat.

There seems to be considerable evidence that wind is one of the dominant physical factors in mountain climates in general, as will be recalled in connection with what was said concerning air movement under the climatic environment. There is a huge literature on the effect of this factor on the growth-form of alpine plants, where the results are very marked; this has been treated for Ktaadn by Harvey. Animals, on the other hand, adapt by functional response or mores (Shelford) rather than by structural changes. This seems suggestive that the restriction of small birds largely to the forest itself, while the small mammals are equally or more abundant on the upper slopes, may be a response to the physical factor of air movement, which thus acts as a restrictive factor in the local distribution of these animals. In this connection it may be said that there appears to be some evidence of the action of this factor on the distribution and response of certain Ktaadn insect types, as will be seen later.

*Pardosa groenlandica* (Rock) Associes .

As a type area for study of pioneer animal conditions, a station, to be known in this discussion hereafter as Station A, was established on the northern slope of the mountain, at an elevation of 4,800 feet and studies made here were supplemented by other studies made in similar habitats. This area, which has been fully described from a geological standpoint by Smith and Sweet (1924) was several acres in extent, large enough to be typical of much biologically similar territory in the upper areas. The surface consists of small rocks, partly rounded by the processes of weathering and attrition, interspersed with some larger ones and with a few large boulders scattered here and there. The surfaces of the rocks, large and small, are largely covered with crustaceous lichens, and to these and to some foliaceous forms and some lithophytic mosses the vegetation is chiefly limited. These plants are characterized as pioneers by their independence of other forms of life, either plant or animal. A slight invasion of alpine tundra has occurred in the form of isolated islands, small in extent, among which the growth of deer-hair (*Scirpus caespitosus*) is most conspicuous. The characteristic plants are the crustaceous lichen *Buellia geographica*, which is the most abundant plant; the foliaceous lichen *Umbilicaria*; and the mosses *Andreaea petrophila*, *Rhacomitrium sudeticum* and *R. acidulare*. This is an area of considerable slope and rapid drainage has not permitted the retention of much water or of the granitic fragments of erosion which are the forerunners of soil. It is also an area of great exposure to the high winds and of great temperature variations within short distances (Smith and Sweet).

Important effects may be accorded to certain animals of the rock area, whose influence on the scant granitic soil produced by the erosion of the rocks, must be similar to those mentioned above as produced by tiger-

beetles and digger-wasps on lake beaches (Shelford, 1913). Judged by these standards the influent animals of the *Pardosa groenlandica* (Rock) Associes are: *Pardosa groenlandica* (Th.), *Lepthyphantes* sp., *Epeira carbonaria* L. Koch, and possibly *Caecilius* sp., the last, however, being a resident phytophagous form.

Certain other forms are predominant to the extent of being conspicuous from numbers, and hence giving a characteristic aspect to the associes. These have a less direct effect on the habitat, and some of the more conspicuous are undoubtedly wind-blown from adjacent habitats. Such forms are not important, and their influence on the habitat is distinctly lesser. They are therefore called subinfluents. Here may be listed *Circotettix verruculatus* (Kby.) and *Upis ceramoides* (L.), together with certain cicadellids and aphids.

This animal population is hardly more varied than the plants, but very interesting in its relationships. An examination of the lists of species (of which only characteristic predominants are given above) shows them to be made up of two distinct elements, local animals characteristic of the area, and winged visitors coming or blown from adjacent communities. These, in turn, are divided into two groups, phytophagous and carnivorous. The phytophagous animals which are at home in this community appear to be: first, the psocids, which, with their cocoons, were common on the undersides of rock, where they breed. They are lichen-feeders, and must find abundant food. The snapping locust is given by Morse (1921) as a form partial to such areas. Probably most or all of the other phytophagous forms are true inhabitants of adjacent tundra or krummholz areas. The spiders form an interesting group in this associes. The webs of *Lepthyphantes* are found in rock crevices, protected from the winds. Of *Epeira carbonaria* Emerton (1914) says that it makes "a round web between the stones which it closely matches in color, and among which it falls at the slightest jar." The large *Pardosa groenlandica* is a true inhabitant of this rock region and, like the last named species, is very sensitive to footfalls on the rocks, disappearing into crevices when disturbed.

It will be seen that the animal population which lives as permanent residents in this pioneer stage is represented by few species. The native phytophagous animals could hardly supply food for the several species of predaceous forms, but a continual stream of visitors (perhaps blown) from the neighboring more richly populated areas seems to supply their needs.

#### Deltocephalus (Sedge) Associes

Unforested area, apart from rock surfaces, occupies a large extent of the upper fifth of Ktaadn, and shows several aspects. Its alpine nature is indicated by the presence of *Dispensia lapponica*, *Rhododendron lapponicum*, *Salix uva-ursi* and *Arctostaphylos alpina*, all found frequently in exposed situations.

Early stages in tundra development appear in many places where soil, beginning to accumulate among boulders, is able to support fruticose lichens, such as *Cladonia*, mosses and liverworts such as *Bazzania trilobata*.

For the study of these conditions a station was established on the alpine tundra of the tableland below the summit, at an elevation of 5,060 feet (Fig. 1). Two pioneers among vascular plants, *Scirpus caespitosus* and *Arenaria groenlandica*, which appear at the earlier stages, have largely disappeared with the increasing acidity of the raw humus which develops from vegetation under low summer temperatures. Various sedges and grasses have formed a definite turf. Xerophytic mosses also are frequent, a few lycopods, and *Potentilla tridentata*. Less commonly occur *Prenanthes nanus*, *P. Bootii* and *Solidago macrophylla*. In this stage of tundra development a very large proportion of the plants are cryptogamic or anemophilous. To the latter the high winds are decidedly beneficial in transportation of pollen and seeds. Of the forms enumerated only *Arenaria*, *Potentilla* and—for pollination only—the less frequent *Prenanthes* and *Solidago* are dependent on animals.

For the purposes of this discussion, it will not be wise to attempt a detailed division of the plant associates of the early and late tundra series. Abundant lichens are: *Cetraria islandica*, *Cladonia rangiferina* and *C. alpestris*. *Polytrichum* is present in several species. *Lycopodium Selago* is conspicuous in rock crevices. Dominant tundra forms are *Juncus trifidus*, *Deschampsia flexuosa*, *Scirpus caespitosus*, and the flowering plants *Arenaria groenlandica*, *Potentilla tridentata*, and *Solidago cutleri*. Subdominant species include *Hierochloa alpina*, *Carex brunnescens* and *C. rigida Bigelowii*. *Diapensia lapponica* and mats of *Salix uva-ursi*, *S. herbacea* and *Arctostaphylos alpina* occupy considerable areas. In the later stages of tundra development *Vaccinium uliginosum* and *Vitis-Idaea minus* dominate, while *Kalmia polifolia*, *K. angustifolia* and *Ledum groenlandicum* constitute extensive stands in many places.

Turning now to the animal associates of the tundra, and to Station C in particular, the increase in number of species of animals over plants in this first step of succession is greatly marked, and considering that the plant list is probably much more nearly complete than the lists of animals, this fact is even more striking. A large number of groups are represented, and animals of all habits of life, phytophagous, predaceous, and parasitic. This associates, much more than was the case with the preceding one, is a self-sufficing unit, a literal microcosm (Forbes, 1887). It might almost be said that, whereas a scarce, little varied biota existed on the rock areas, the increase of plant variety by arithmetic ratio on the early tundra had been accompanied by an increase of animal variety in algebraic ratio. The selection of predominants is rather difficult, since probably no single species dominates the habitat as, for example,

some plants dominate their habitats. But the most numerous animals, which by their numbers probably produce the maximum animal effect on the habitat, are undoubtedly the cicadellids, which are present in large numbers and some variety. There is besides a considerable population of other phytophaga, among which certain aphids are noticeable, but neither for numbers nor variety do they approach the leaf-hoppers, of which a number of undetermined species have been noted.

Animal subinfluents, exerting a degree of influence on the sessile plant dominants by eating foliage, or affecting the numbers of phytophaga by preying on them are, in part: *Deltocephalus pulicaris* Fall., *Cymus luridus* Stal., *Aphis* sp., *Epeira displicata* Hentz., *Pardosa muscicola* Emerton.

Subinfluents, generally less numerous and exerting influence to a lesser degree are: *Macrosiphum pisi* Kalt., *Psylla* sp., *Elasmotethus cruciatus* (Say), *Rhopalosiphum* sp., *Phaeogenes hemiteloides* Ashm., *Acidota crenata* (Fab.).

Predominants, present in such numbers as to be conspicuous, but whose relations to the biota of this associes are not sufficiently well known to admit of more detailed ecological classification, are: *Coenosia nigrescens* Stein., *Mitopus morio* Fab., *Acropiestia* sp., *Micropterys montinus* (Packard), *Clepsiorthus assiduus* (Cress.). Of less importance appear *Megaselia rufipes* Meig., *Schoenomyia litorella* Fall., *Asaphes americana* Gir., *Salpingus virescens* Lec., *Epurea* sp., *Aenoplex betulaecola* Ashm.

It will be seen that a considerable number of predaceous forms feed on the plant-eaters. Among these the Pardosas are most abundant. Other spiders and nabids are also present, and a large number of parasitic Hymenoptera. The only strata are ground and herb, but characteristic ground-dwelling animals were less abundant than herb-living forms. Only two species of ground-beetles were taken, one in the larval stage, and two staphylinids. A careful search for animals dwelling in the ground was very scantily rewarded. During the summer apparently most of the animals of the shallow soil leave it for life on the surface.

#### *Cymus discors* (Sedge-Heath) Associes

Representing transition between the life of the early and late stages of tundra animal communities, an area, to be known hereafter in this discussion as Station C-2, was selected. This was near the summit and consisted of mixed patches of grassy tundra, intermixed with heath plants, the latter representing the later condition of tundra. This area, as well as others similar to it, was examined by the usual methods of collecting and study.

Subinfluents: *Cymus discors* Horv., *Lygus pabulinus* (L.), *Hyperaspis bigeminata* (Rand.), *Amblyteles promptus* (Cress.), *Melanoplus femur-rubrum*

(DeG.), *Macrosiphum* sp., *Meadorus lateralis* (Say), *Calophis* sp., *Euceraphis* sp., *Elater moerens* Lec., *Crepidodera helxines* Lec.

Subinfluents (less numerous than those listed above): *Melanoplus mexicanus atlantis* (Riley), *Botanobia frit* L. var., *Winthemia 4-pustulata* Fab., *Bothriothorax novaboracensis* Howard, *Spilocryptus cimbivorus* Cush.

*Predominants* (prominent in the associates aspect): *Coenosia flavicoxa* Stein., *Hypocera clavata* Lowe., *Scatella lugens* Lw., *Phora aterrima* Meig., *Melanochelia tetrachaeta* Mall., *Berycyntus* sp., *Thanasimus dubius* (Fab.), *Perilampus stygicus* Prov. These are listed in approximate order of abundance.

Judging from the collections, it appeared that the predominant (in the general sense) animals were in about the same variety as in the sedge tundra. The more varied plants support an extensive population of phytophaga, among which no single group seems to stand out with the prominence of the cicadellids in the last associates. The red-legged grass-hopper is a common form and is listed among the subinfluent species, since it is present in sufficient numbers to influence the habitat through its feeding on the foliage. Stink-bugs, leaf-bugs, four species of click-beetles, two of leaf-beetles and two of sawflies feed on the plants. There is some evidence, however, that the animal associates revolves about the various aphids, which are present in considerable numbers. There are several genera and probably several additional species, sufficiently numerous to be very prominent in collections taken by sweeping among the heath plants. The number and character of the predaceous forms taken is also in accord with the conception of aphid predominance among the animals. Six species of ladybugs, one of which, *Hyperaspis bigeminata* (Rand.), should be assigned the status of an animal predominant, the neuropteran *Leuctra* and a number of parasitic Hymenoptera, including braconids and ceraphronids, have been collected from this community; these are all known to prey on aphids either in the adult or larval stage or both. The ground-beetle *Amara* was taken running on the ground, and seems to be rather characteristic, the various Diptera less so. Midges, fungus-gnats, syrphids, hump-backed flies and anthomyiids are constant here, and the last two are possibly to be considered as numerical sub-influents.

#### *Pardosa uncata* (Heath) Associates

The heaths mark the climax in tundra vegetation. Plant distribution is very irregular. Previous note has been made of a few species characteristic of locations of great exposure and thin soil, such as *Diapensia*, Lapland rhodora and alpine bear-berry. Many more species are found in slightly more favorable conditions. *Vaccinium uliginosum* is the plant dominant

in large areas. *V. pennsylvanicum angustifolium*, *Kalmia polifolia*, and *K. angustifolium*, each have areas over which they are respectively dominant. *Vaccinium Vitis-Idaea minus*, *Empetrum nigrum*, and *Ledum groenlandicum* are very abundant. Here, of course, pollination is dependent on insect life, which will be seen to be sufficiently abundant. The fruits of the ericads, as in the preceding stage, furnish a very considerable food supply.

Subinfluents: *Pardosa uncata* Thorell, *Mecostethus lineatus* (Scudder)<sup>1</sup>, *Athysanus arctostaphyli* Ball<sup>2</sup>, *Athysanus elongatus* Osborn,<sup>2</sup> *Platymetopius acutus* (Say)<sup>2</sup>, *Anatis 15-punctata* (Oliv.), *Coccinella transversoguttata* Fald.

Subinfluents (less numerous than the above): *Pheletes* sp., *Chloropisca glabra* Meig., *Formica sanguinea* var. Only a small collection of animals was taken from this station, of which the predominant species are listed, together with a considerable number of records taken from the literature on this or similar areas of the mountain. Predominant animals appear to be cicadellids of several species, with the spider *Pardosa uncata*. *Athysanus arctostaphyli* and *A. elongatus* are particularly characteristic as feeding on the dominant plants. In the ground was taken *Pheletes* larvae and under loose stones the ant *Formica sanguinea* var. Two species of coccinellids no doubt feed on small insects that infest the dominant plants. The fly *Chloropisca* belongs to a family largely characteristic of meadows and is perhaps an immigrant—or blown in—from the grassy tundra.

#### *Linyphia nearctica* (Krummholz) Associates

Where slight depressions in the expanse of the tundra have accumulated sufficient humus and offered initial protection from wind, fir and spruce have developed as definite islands. These two forms, *Picea mariana* and *Abies balsamea*, in separate stands, cover large areas on the saddle and the slopes above. So closely do the individual trees grow that it is difficult to force a passage through them (Fig. 2). The extreme stature is attained at the most western point of the "saddle" (Harvey, 1903a), where the trees approximate ten feet. Here then, as over the entire mountain and in the lowland of the immediate vicinity, the climax plant stage is *Picea-Abies* forest.

The shade of the close-growing trees is so thick that in many places there is practically no forest floor vegetation. Where mosses appear, a means of retaining moisture is furnished. In such a situation the death of a tree offers a wind-protected, well-watered opening. Such a spot becomes populated with plant species characteristic of openings in the

<sup>1</sup>Morse (1921).

<sup>2</sup>Osborn (1915).



coniferous forest at lower levels. *Amelanchier oligocarpa* is fairly common. Although seasonal societies are not sharply differentiated as a rule, on account of the low temperatures that persist throughout the summer, *Linnaea borealis* var. *americana* is conspicuous only in June. The most abundant species growing on the forest floor are *Chiogenes hispidula*, *Oxalis acetosella*, *Cornus canadensis* and *Trientalis americana*. Associated with them are *Clintonia borealis*, *Maianthemum canadense*, *Coptis trifolia* and *Streptopus roseus*.

The low-growing trees, twisted close to the ground, which constitute krummholz, offer protection to small mammals such as squirrels and hares. They present mechanical obstructions against pursuers, whether cursorial mammals or raptorial birds. Their dense shade and the continuous evaporation from the moss about their roots afford equable atmospheric conditions in contrast with the rapid fluctuations of these and other climatic factors in more exposed parts of the mountain. If the fruits, leaves, bark and roots of the immediate stand do not furnish sufficient food, plenty can be obtained among the heaths of the adjacent tundra.

Subinfluent: *Podisma glacialis* (Scudder)<sup>1</sup>, *Gnathosa brumalis* Th., *Theridion zelotypum* Emerton<sup>2</sup>, *Epeira displicata* Hentz, *Notolophus antiqua* L. (juvenile), *Linyphia nearctica* Banks.<sup>2</sup>

Subinfluent (less numerous than the above): *Neuratelia scitula* Johannsen, *Cystoma pilipes* Lw., *Lycosa* sp., *Scatophaga furcata* Say. The last named could be perhaps best considered as a dominule or subdominule, frequenting the microhabitats supplied by decaying fecal or other organic matter. They are by no means confined to this associes.

The krummholz vertebrates have already been considered. The invertebrates have been less studied than those of some of the other associes; collections made include the forms given. Particularly characteristic are the spiders; *Gnathosa* was taken under stones and in the thick moss, in which it habitually occurs. Two species are listed by Emerton (1920) as particularly characteristic; it will be seen that these, together with a young *Epeira* which the writer found very abundant, are both spinners. *Theridion zelotypum*, according to Emerton, "spins large, coarse webs between the spruce branches, with nests in which the female and her brood of young live." *Linyphia nearctica* is also found on spruce. The irregular, delicate strands of the young *Epeiras* were found by the writer on a warm August day abundantly stretched between the tips and branches of the semi-prostrate, breast-high conifers. The krummholz thus is seen to furnish the first habitat in succession which supplies favorable conditions for any general and varied population of spinners, the few species of this habit found heretofore being confined to spaces between

<sup>1</sup>Morse (1921).

<sup>2</sup>Emerton (1914).

rocks or among low heath plants and grasses. Among the krummholz, on the other hand, the branches of the alpine trees furnish a place for attachment of webs, while the thickness of the growth to some extent protects them from the force of the excessively strong winds.

On the forest floor, we find besides *Gnathosa brumalis*, two lycosids, one of which was fairly abundant.

Thus we see in the krummholz, as illustrated by the spiders, for the first time occurring a definite stratification of animals into societies, a thing not possible in the earlier biotic associates, with their shallow soils and low herb cover.

Another characteristic animal of this community is the White Mountain wingless locust (*Podismalacialis*).

Fungus-gnats (*Neuratelia scitula*) and dance-flies (*Cystoma pilipes*) are abundant under the dense shade of the scrub, where conditions for the former are particularly suitable. Two species of anthomyiids and two of sapromyzids were taken, and their larvae no doubt feed on the abundant decaying vegetable matter. The caterpillars of *Notolophus antiqua* were taken, one of the few Lepidoptera taken or observed in the upper stations, whose high rate of air movement is perhaps less suitable for insects of this character. Among the Hymenoptera are Ichneumonidae, Belytidae and Scelionidae; the second are known to parasitize dipterous larvae.

#### *Rheumaptera hastata* (Upper forest) Association

A small collection of animals was made in the upper regions of the climax forest, between Chimney Pond (2,900 feet) and the foot of the steep slide leading up to the plateau and upper stations. The plants are similar to those described below for Station E; this upper climax forest will be known as E-2. The invertebrates taken are listed.

Subinfluent (probably none affecting directly the true sessile dominants): *Rheumaptera hastata* L., *Argynnis atlantis* Edw., *Malacosoma disstria* Hon. (juvenile), *Hepialus mustelinus* Pack., *Acronycta* sp. (juvenile), *Psocus* sp., *Platynus sinuatus* (Dej.), *Galerucella cavicollis* (Lec.), *Coccinella* sp. (juvenile), *Simulium venustum* Say.

Here psocids were abundant, feeding on lichens. The ground beetle *Platynus sinuatus* was taken among stones and mosses on the ground, and the leaf-beetle *Galerucella cavicollis*. On the forest floor occurred the larva of one of the coccinellids. Three species of Lepidoptera were taken from this station, the spear-marked black (*Rheumaptera hastata*), swift (*Hepialus mustelinus*) and a dagger (*Acronycta*). The number of these and other Lepidoptera in the climax forest, as contrasted with the great scarcity of this order at the upper stations, suggests that, as in the case of the birds, air movement may be a factor in their local distribution.

This is almost certainly the case with species like the swifts, which even in the forest do not appear to fly usually at any great height. The spear-marked black was an abundant species throughout the lower forest, but was not observed or taken at any of the upper stations.

*Sciurus hudsonicus* (Spruce-Fir) Association

The studies were mostly made in the climax *Picea-Abies* forest of the South Basin at Basin Pond. The elevation was 2,400 feet, high enough to illustrate the biota of the mountain sides up to the level of the slides. The station, known as Station E, was situated on a moraine ridge a few rods back from the swampy shore of the pond; in some places *Thuja* ran to the edge of the water. In other spots a strip of *Chamaedaphne* intervened. The ridge itself consisted of a soil of decomposing *Spagnum*, from which projected glacial boulders and partly buried rocks. The characteristic plants were *Picea* and the abundant and profusely-blooming *Kalmia angustifolia*, *Viburnum cassinoides*, *Amelanchier oligocarpa* and *Nemophanthus mucronata*.

From the plant standpoint, this region is the most mesophytic under consideration in this study. While Basin Pond itself is swept by heavy winds, the surrounding forest offers to animal life ample protection from storms. Food is abundant in berries, seeds, bark and leaves of many kinds. Inaccessibility for human beings may be mentioned as another factor making for seclusion, of importance particularly to the larger animals. As has already been discussed in detail, practically all the vertebrate life in general, and the bird life in particular, center in this part of the mountain.

Subinfluents: *Serropalpus barbatus* (Schall.), *Agelena naevia* Walckenaer, *Amaurobius sylvestris* Emerton, *Epeira trivittata* Keyserling, *Zilla montana* Koch, *Syrphus torvus* O. S.

Subinfluents (less numerous than the above): *Mesopsocus unipunctatus* Müll., *Pogonocherus penicellatus* LeC., *Papilio turnus* L., *Eupethicia* sp., *Leptomeris inductata* Gn.? (juv.), *Olethreutes* sp., *Colias philodice* Godt., *Sarcophaga aldrichi* Parker. (Perhaps the last named should be classed as a dominule, whose true ecological position is that of a predominant in the microhabitat furnished by the decaying body of a dead animal).

Predominants (conspicuous in the habitat, but not further classified ecologically): *Fannia canicularis* L., *Chrysops sordida* O. S., *Camponotus* h. p. *ferrugineus* Fabr., *Aedes fitchii* Felt, *Culiseta impatiens* Wlk., *Platyura subterminalis* Say, *Prosimulium hirtipes* Fries., *Chrysops niger* Macq., *Tabanus astutus* O. S. var., *Xylota curvipes* Loew., *Tinea* sp.

The invertebrates listed are those more prominent in the collections and records. Faunistically they form a rather interesting combination

of alpine and sub-alpine forms with species widely distributed at lower levels. Ecologically the invertebrate predominants appear to be spiders of eight genera and eleven species. There are also two species of ground-dwelling phalangids and two of ground-dwelling mites, so that the arachnid population of the forest floor of this associates is very large and varied. Many live on the mossy ground under the thickly growing conifers and among the crevices of the numerous rocks. In such places are found the rough webs of *Amaurobius*. In scrub, or attached to dead limbs or stubs at that level, we find the orb-webs of *Epeira trivittata*, and *Agelena naevia* builds its funnel-shaped webs among low herbs in openings in the forest. Among the low trees are found the imperfect orbs of *Zilla montana*. The distinct stratification of the spiders, especially the relatively large numbers of ground dwelling-forms, is of interest. One of the dominant physical factors in this as in the other mountain habitats is the strong wind. It is certain that the spinners of erect orbs are at a disadvantage in such conditions, as compared with those which either run down their prey like the *Lycosas* or build low, little-exposed webs like *Amaurobius* and *Agelena*. It was observed that the webs of *Epeira* were soon torn to pieces by the wind.

The insect population is large, both in individuals and species and only certain species will be given particular discussion. In openings of the forest the Locustidae were abundant; the two-striped locust, the northern locust and the banded locust all being taken near the forest margins of artificial clearings; none of these are forest species. Particularly characteristic of such moist forest conditions are the two Cicadellidae, *Deltocephalus sylvestris* and *Graphocephala coccinea*, found feeding on many plants of the lower forest strata. In the ground-stratum was found the staphylinid *Antobium pothos* and the larva of a cephaloid. A number of other beetles were collected, of which the most characteristic appeared to be the cerambycid *Pogonocherus*. In this moist forest station Diptera were very abundant. Tipulidae were common, three genera and species being represented. Four families, whose relations to man are such as to bring their activities much to his attention were unfortunately prominent in the community: the Culicidae were represented by *Aedes fitchii* and *Culiseta impatiens*; the Tabanidae by two species of Chrysops and one of Tabanus; the Simuliidae by *Prosimulium hirtipes*; and the Muscidae by *Musca domestica*. The last named was a man-brought importation due to lumbering operations, but the others are typical and numerous in the natural habitat. Here were found two syrphids, *Syrphus torvus* and *Xylota curvipes*, while the Myceteophilid *Platyura subterminalis* was abundant in favorable spots locally.

The most interesting feature of the habitat was the relatively large number of Lepidoptera as compared with those found in the upper stations.

Eight species were collected, and probably a dozen in all were seen. Evidently the climax forest is the true montane home of this group in general and only hardy species or individuals can cope with the conditions of the open tundra, where they are never abundant.

In general, we may say that the spruce-fir climax shows, by its animal as well as its plant life, that it is in part a wave of upward-pushing biota from the more temperate forest below, invading the lower boundary of the sub-alpine forest. Here we find a large number of species, showing a mixture of the two populations. The climax habitat shows a list of characteristic species, not found in the subclimax stages. These species of the climax are arranged in stratal communities or socies, although this fact was not particularly studied for any group except the spiders; there is no reason, however, to suppose that this stratification does not extend to the whole animal population.

#### Aeschna (Pond-Bog) Associates

Some collecting was done and the conditions were studied in a semi-aquatic community furnished by a pond-bog near Pamola Pond, at an elevation of 2,700 feet. The pond itself is a small body of water, occupying what is evidently an old glacial depression and held in place by the moraine whose glacial structure, indeed, is very plain at one point where it has been cut through by a ditch in aid of lumbering operations. On the eastern and southern sides of this pond the moraine ridge has a stunted growth of spruce and fir, the climax forest of the Great Basin of Ktaadn. On the other sides, the pond is being invaded by a regular sphagnum bog complex, the sphagnum mat overhanging the deep water close to the shore in spots, and being followed by the typical marsh shrubs, among which *Chamaedaphne* is most common; the stunted *Picea-Abies* forest brings up the rear, and the whole seems to furnish a rather typical example of the filling of a glacial pond by vegetation. Northwest of the pond itself, and connected with it by a flooded bog, is a small, shallow bog-pond, where the process of filling has so far advanced as to give the impression of rather a swamp than a pond, and some of the spruce-fir forest nearby is evidently growing on what was once a part of the old pond. The general environment is shown in the illustration (Fig. 3).

From the standpoint of plant succession, the most significant feature of this small sphagnum bog is its possession of subalpine species, such as *Empetrum nigrum* and *Vaccinium uliginosum*, not found elsewhere until the high slopes above the steep ascent are reached.

The greater number of plants are those common to sphagnum bogs of this latitude. The steps in development from an open pond are plain. Sphagnum forms the basis for *Scheuchzeria palustris* and *Drosera* follows, and later *Sarracenia* with *Vaccinium oxycoccus* and *Smilacina trifolia*.

*Carex* is represented by *trisperma* and *pauciflora* *Kalmia* is abundant, especially *K. polifolia*, on the numerous islands of soil rising slightly above the water. Individual trees of *Picea mariana* and *Larix laricina*, stunted and unhealthy looking, represent the encroachment of arboreal forms, frequently on small islands separated as yet from the main shore by narrow aisles of standing water (two or three feet deep in late August). At one point *Thuja occidentalis* appears.

The absence of orchids, noted also for Lake Tear bog on Mount Marcy, is explained by Harvey as due to isolation.

The persistence of subarctic forms completely obliterated from other parts of the lower slopes indicated the tremendously slow development of the sphagnum bog. It is, however, being gradually filled in and surmounted by sufficient humus to support mesophytic forms. Near the advancing trees are beginning to appear such plants as *Osmunda cinnamomea*, *Cornus canadensis*, *Clintonia borealis*, and *Nemopanthus* and *Ame-  
lanchier oligocarpa*.

The air temperature, in the shade and just over the surface of the water varied from 17°C to 20°C, at 3:30 P M on afternoons in August. The temperature of the water, close to shore in the shade of vegetation was 12°C at a depth of 6 inches; at the same depth, but 8 feet out from shore, and therefore in the sun, the temperature ranged between 13°C to 16°C.

Subinfluent: *Aeschna* sp., *Gerris* sp., *Gyrinus affinis* Kby., *Gyrinus lugens* LeC., *Trepobates pictus* (H. S.), *Lestes uncatatus* Kby., *Epeira patag-  
iata* Clerck, *Coccinella trifasciata* L., *Leptura chrysocoma* Kby., *Tetragnatha extensa* (L.), *Misumena vatia* (Clerck), *Philodromus* sp., *Lin-  
nopus rufoscutellatus* Latr. (?), *Hydrophorus pirata* Lw., *Hilara tristis* Lw.

Subinfluent (less numerous than the above): *Misumena asperata* Emerton, *Dolomedes sexpunctatus* Hentz, *Notonecta* sp. (juvenile), *Sinea diadema* (Fabr.), *Euscelsis humidus* (Osb.), *Agabus discolor* (Harr.), *Hydaticus* sp. (juvenile), *Mamestra* sp. (juvenile), *Platypalpus flavirostris* Lw., *Frontina* sp., *Hyalomyodes triangularis* Lw., *Vespula norwegi-  
coides* Sladen, *Zaglyptus incompletus* (Cress.)

Dominules (predominant in microhabitats within the associates): *Aphis spireaphila* Patch (numerous groups on scattered Spiraea), *Sminthurus spinatus* MacGillivray, *Sapromyza sheldoni* Coq. (on decaying organic matter).

Predominants (conspicuous in the associates, but not further classified ecologically): *Chironomus* sp., *Siphylurus alternatus* Say, *Tanytus* sp., *Limnophilus rhombicus* L., *Lispocephala erythroceras* Desv., *Arctocorixa* sp. (juvenile), *Sciara* sp., *Ochthera mantis* DeG., *Diplotaxis versicolor* Lw.

The animal population of this area is listed above (invertebrates) in part only. The list does not indicate, for the animals, any number of

boreal species, though *Coccinella trifasciata* may be so considered (Blatchley, 1910). The habitat showed two strata, water and herb. From the water were taken nymphs of *Arctocorixa*, *Notonecta* *Siphylurus alternatus*, and several species of gerrids, of which one (undetermined) species appeared as one of the numerical predominants. The adults of *Limnoporus rufoscutellatus* and *Trepobates pictus* were taken, the latter being more common; also larvae of a Hydatiscus and three gyrenids, *G. affinis*, *G. lugens*, and *G. latilimbus*, the first two named being predominants. Here also was taken the larva of the pond-lily chrysomelid, *Galerucella nymphaeae*, on the yellow lily, and a trichopterous larva *Limnophilus rhombicus*. In the damp moss and debris around the roots of the swamp-plants, was found the dytiscid *Agabus discolor*.

The stratum of vegetation over the water yielded, to sweeping and individual collecting, a large and characteristic population of swamp animals. The webs of *Tetragnatha extensa* were found on dead branches of dwarf spruce; they contained mostly the remains of chironomids. The crab-spiders *Misumena asperata* and *M. vatia* were found, the latter living and breeding on Kalmia. Young Philodromus and specimens of *Dolomedes sexpunctatus* were also taken from the moist herbage. Emerton gives *Epeira labyrinthica* as characteristic of this habitat.

From the vegetation was taken *Sminthurus spinatus*. Spiraea growing along the edge of the bog was heavily infested with *Aphis spiraeaphila*; *Lygus pabulinus* was swept from the plants, as well as the caterpillar of a noctuid (Mamestra). A large population of characteristic flies were taken in flight or resting on the swamp plants. They included Chironomus and Tanypus, the mycetophilid Sciara, the long-legged fly *Hydrophorus pirata*, the dance-flies *Hilara tristis* and *Platypalpus flavirostris*, *Sapromyza sheldoni*, an ephydrid, *Ochthera mantis*, the chloropid *Diptotaxia versicolor*, the anthomyiid *Lispocephala erythroceras*, and two tachinids, *Frontina* and *Hyalomyodes triangularis*.

Prominent in flight over the water was the dragon-fly *Aeschna*, while the stalk-winged damsel-fly *Lestes uncatulus* was abundant along the shores of both ponds.

Other species taken in this habitat, mostly by sweeping from vegetation, are *Eucelis humidus*, from the heath-plants; the spiny assassin-bug, *Sinea diadema*; an aphid, Macrosiphum: *Coccinella trifasciata*; an ichneumon-fly, *Zaglyptus incompletus*; two species of saw-fly larvae; and the wasp *Vespula norvegicoides*. Here was taken the old tussock-moth, *Notolophus antiviva*. The beetle *Mezium americanum* was probably introduced by the establishment of the lumber camp at Basin Pond, not far away.

The pond-bog community shows in general an assemblage of animals common to such habitats at all levels and in all types of forma-

tions. It is a distinctly local habitat, composed of characteristic species with characteristic mores, and is to that extent ecologically distinct from the coniferous forest climax which surrounds it. It is no doubt undergoing gradual succession, as is indicated by the vegetation, to the climax forest; this process was not studied for the animals, the time only permitting a survey of the most characteristic bog conditions. Enough has been done to indicate that the community is distinctly a local one, with an animal population distinct in composition and mores from that of the surrounding climax, by which, no doubt, it will eventually be succeeded.

### The Steep Slide Animal Community

A small collection of animals was made, and the conditions briefly noted, on a steep slide leading from the head of the South Basin up to the tundra of the saddle. This station was at an elevation of 3,450 feet. The slope, which was as steep as rocks and earth would lie, was covered in the lower part by washed-down granite detritus, farther up by rocks. Save for lichens, vegetation on the slide itself was practically absent. The sides, however, are being invaded by various plants, among which *Solidago*, *Epilobium* and *Alnus* may be noted, with the usual rear-guard of krummholz spruce. This station showed a rather curious mixture of animals from the extreme stages of succession in both directions. The dominant animal appeared to be *Pardosa groenlandica*, a bare rock species also dominant in Station A. On the other hand, this was the highest station for the amphibians, the common toad (*Bufo americanus*) being observed here. It is known to exist otherwise only in the climax forest, but was here no doubt associated with the upward extension of that forest on the steep slopes. The caterpillars of *Malacosoma disstria* were heavily infesting stunted birch, and the cicadellid *Oncopsis* was found feeding on alder. The former was found otherwise only at levels below this station; the spider *Lycosa albobastata* was found here, and also above on the alpine tundra, while the harvestman *Mitopus morio* and the ubiquitous humble-bee *Bremus terricola* occur both above and below; the latter appeared here on the goldenrod. It might be expected that these steep slopes would be a tension line between the animals of the upper plateau tundra and those of the climax forest, but it is interesting to see how well this is indicated by the presence in the same station at this level of animals as ecologically diverse elsewhere on the mountain as *Pardosa groenlandica* and *Bufo americanus*. No doubt this partly explained by the fact that at this level the forest advances directly onto the bare area, without intervening tundra stretches that occur with the shallower soil and greater wind exposure of higher altitudes.



## DISCUSSION AND SUMMARY

The climate of Mount Ktaadn, as far as we have actual or inferred knowledge of it, is a rather typical montane climate, showing low mean and minimal temperatures, heavy precipitation and high winds, the last associated with high evaporating power of air. These factors are operative in all areas studied, but show a general increase with altitude and exposure. It is an entirely different climate from that of the low country coniferous forest lying around the base of the mountain and likewise entirely different from the climate of the tundra regions lying near sea level farther north (Fig. 9). Its hythergraph does not show similarity to either of these, although they overlap somewhat during the warmer part of the year. It is much cooler at all seasons of the year than the former, but never reaches the extremely low winter temperatures of the latter. The precipitation is greater than that of either.

From the standpoint of both ecology and faunology, these facts seem significant. There are a number of species found at high altitudes on the northeastern mountains, which are considered as boreal or possessing northern affinities, that is to say, they are identical with, or more or less closely allied to, species living much farther north at lower elevations. We have generally considered that these species, of general distribution at low altitudes during the southern extension of the ice-sheet, found on the retiring of the glacial margin the same climatic conditions at high altitudes that occurred farther north near sea-level, and hence these arctic-alpine areas became refuges for groups of boreal species which were, as it were, left stranded on the mountain-tops. It is interesting to see that the conditions in these areas, as represented by the hythergraphs based on the Mount Washington data, appear those of a climate decidedly different from that of the Ungava regions. Since the species appear to be structurally constant in both places, there must have occurred physiological differentiation and such species are perhaps to be considered as physiological ones. Undoubtedly what is needed here is a study of the physiological life histories (Shelford, 1913) of the same species occurring on the high tundra of the New England mountains and the low tundra of the regions lying farther north. Such information is at present entirely lacking, but a similar phenomenon has been investigated for species of Cicindellidae living both in Illinois and Manitoba; in this case there was a distinct correlation between the life histories of these two widely separated groups of individuals of the same species, and the climatic conditions respectively operative.

Mingled with these truly alpine animals are a number of other forms of general distribution in the northern coniferous forest climax at lower levels, or of even wider distribution, and the population is a mixture of these two main types. This entire population, or series of animal

communities, is involved in a process of succession, by which, as the naked and eroding rock at all levels is gradually becoming covered by the climax forest of the region, the characteristic animals of the areas involved are also undergoing corresponding and progressive changes. The process is complex, involving as it does biotic, edaphic and climatic factors, respectively operative to different degrees in the different stages and under various local conditions. In general it may be said to consist of the following successive associates, leading gradually to the animals of the climax forest:

A biotic community capable of living on bare rock, in the practical absence of soil. The plants of such a community are chiefly lichens, and are independent of animals. The resident animals are forms capable of living on the sparse plant growth, or predaceous forms, including a number of highly characteristic spiders. This community is probably not self-supporting, from the animal side, but its predators depend in part for food on insects blown from adjoining regions. It is distinctly a one-stratum community, subterranean or rather sub-lithic, in part a response to the climatic factor of air movement. This has been referred to as the *Pardosa groenlandica* (Rock) Associates.

A biotic community consisting of the turf of alpine grasses and sedges that come to occupy the first thin soil formed by erosion and the decay of previous organisms, and its animal inhabitants. This shows a considerable increase in plant variety, and a more marked increase in animal variety, consisting of numerous phytophaga and their enemies. It appears to be a self-sufficing biotic community, a microcosm. It is the result of changes, principally physiographic but in part biotic, from the previous community, and is still to a large extent a one-stratum complex, the herbs and their inhabitants. If designated by the group of animals which are certainly most numerous in species and individuals, this stage would be called a cicadellid associates, the *Deltoccephalus* (Sedge) Associates.

A biotic community composed of the alpine heath-plants which thrive with the accumulation of a better and a deeper soil, and the associated animal population. This community is also self-sufficient consisting of a varied population of phytophagous forms and various predaceous species. It has been evolved from that just described by a series of changes in which the biotic factors have probably been progressively more important, the physiographic ones less so. It is difficult to fix upon animal predominants sufficiently characteristic to be used in naming this associates, but the *Cymus discors* (Sedge-Heath) Associates has been suggested.

A biotic community consisting of krummholz coniferous forest and its animal denizens. This has been produced from the preceding stages by a complex of factors, which are, however, probably chiefly edaphic and biotic, rather than climatic. The animal population is to a considerable

extent that characteristic of climax coniferous forest, but some large vertebrates are lacking and there are highly characteristic invertebrates. This is a stratified animal community, but the herb society is scanty or missing and the tree stratum is hardly higher, in many places than the shrub society of other forests. From a characteristic animal, this is called the *Podisma glacialis* (Krummholz) Associates.

A biotic community consisting of the climax spruce-fir forest and its associated animals. This is a well-stratified and established formation, whose existence on the area it occupies will be very long under natural conditions. Its evolution, like that of the krummholz, has been edaphic and biotic, rather than climatic, but it is in itself a climatic climax. Under usual conditions, it would be (that is, when not subjected to attacks of such forms as the spruce bud-worm), difficult to name animal predominants; indeed, no animal usually found there dominates the habitat as the forest itself does. But if this association is to be named after one of its highly characteristic animals, it could be called the *Sciurus hudsonicus* (Spruce-Fir) Association.

#### CONCLUSIONS

The animals of alpine tundra communities show a definite succession, beginning with the communities inhabiting bare or lichen-covered rocks, and passing through subclimax stages until the climax association is reached in the animal community of northern coniferous forest.

This succession includes a gradual change in the animal life, especially as regards species; animals abundant in the earlier associates being absent in the later ones, and vice-versa, and the intermediate stages showing a more or less gradual falling off of earlier species and increase of later ones.

The various animal tundra communities are characterized by predominant or at least characteristic animals with different types of habits or mores, and these, in so far as they have been studied, show an adaptation response comparable with the structural responses of plants under similar conditions; this may be exemplified by the habits of the Pardosas, dominants of the rock animal associates, with those of the Epeiras, first prominent in the forest stages of succession.

The factors influencing the transformation of the earlier associates of tundra are probably largely biotic and edaphic, since the climatic differences of the various tundra areas cannot be decisive, although they have not yet been measured instrumentally. There is every reason to suppose that the animal associates are in the main determined by the plant associates, and that the reverse condition, has been important only indirectly. The indirect effects of the subinfluent consist at least in contributing their dead bodies to the enrichment of the soil.

On the other hand, the physical differences between the tundra environments as a group and the climax and subclimax forest stages appear to be considerable, especially as regards air movement, and may possibly have exerted a decisive influence on certain animals, confining them to the later (forest) associations.

The factors influencing succession over the various tundra areas have been only to a limited degree operative in the case of certain animals, especially but not exclusively vertebrates, and more especially the smaller mammals; such animals show less restriction to the boundaries set by various invertebrate and plant associates, or none at all.

## ANIMAL ECOLOGY OF MAINE PINE-HEMLOCK FOREST

### SCOPE OF WORK

Of the papers cited in the introduction as dealing in a quantitative way with the ecology of land animal communities, the most elaborate and the one covering the longest period of time is that of Weese (1924). This author, using recording instruments to measure the factors of the physical environment and the method of "quantitative sampling" for the study of the animal population, carried his work throughout the year. His paper presents a very complete account of the annual climatic and biotic cycle of the elm-maple forest where the work was done, the stratal and seasonal societies and their dominants, and the correlations between environmental changes and animal response.

The present portion of this study gives the results of an attempt to apply the same method to the study of the animal ecology of northern coniferous forest. This was of necessity a short-time study, embracing the summer months of 1923, during the latter part of which the most extensive of the biotic studies were made. It is not therefore to any degree a study of seasonal societies, but it is hoped that it will give some idea of the stratal societies and the physical conditions existing in coniferous forest for comparison with those of the deciduous forest as described by Weese for the same period of the summer. A rather large part of the work is concerned with the physical conditions of the habitat. As these are little known it was deemed best to devote a considerable portion of the limited time available to their investigation and the accumulation of instrumental data on the subject.

As it seemed hardly likely that the succession of climatic changes, through so short a period and at this time of the year, would be very marked, particular emphasis was laid on the question of stratification of these conditions, and the instruments were exposed with this in view. The environment was investigated in terms of stratification of temperature, humidity, evaporating power of air, and light. Some of the instruments used not being of the recording type, recourse was had to the expedient of reading them several times a day at periods considered as critical in meteorology.

The biotic data was obtained by the method described by Weese as sampling. It will be discussed in detail later. For the present it may be said that the collecting consisted in taking samples of the animal population of the strata where the physical factors were being instrumentally meas-

ured; the methods of taking these animal population samples were at all times kept uniform. It was not, however, possible to take and study these samples as frequently during the early part of the summer, because of the limitations of time imposed by other duties. For this reason the biotic studies for the month of August are more complete than those preceding.

The birds were not considered in the present study, which from the very nature of the collecting, chiefly concerns invertebrates. The area studied was trapped from time to time, however, to get some idea of the mammals present and their relative abundance. The results of this will be included in a separate portion of the discussion. The forest is too near cultivated areas and too much subjected to human influences, to make the findings on the mammalian population of more than local interest.

#### ENVIRONMENT.

The area studied is a heavy growth of white pine (*Pinus strobus*), Norway pine (*P. resinosa*) and hemlock (*Tsuga canadensis*), comprising a part of the forest under the charge of the Forestry Department of the Agricultural College of the state university at Orono, Maine. The stand consists of mature trees of large size and, while not virgin, has never been completely cut off, although individual trees have been taken out here and there. A little birch and alder occur, also a few young maples and white ash. The area is southeast of the university campus, and adjoins farm land on some of its irregular boundaries, while on others it is bounded by swampy land covered with young second growth deciduous forest. The elevation is about 115 feet, and the relief is slight, but with a little slope to a swampy brook in the eastern portion.

The undergrowth is scanty; individuals or small stands of a single species constitute the discontinuous vegetation. The intervening ground is covered with a thick carpet of coniferous needles, twigs and other organic debris. The shrub stratum is especially poorly developed. The number of plant species present is increased by the influence of open fields on two sides, south and west. The swamp and young forest on the northeastern boundary contribute a few forms not characteristic of the area as a whole.

Relatively few species of shrubs and herbs were noted in the vicinity of the stations. The shrubs were *Corylus rostrata*, *Rubus alleghaniensis*, *Lonicera canadensis*, *Ribes lacustre* and *Spiraea latifolia*. The most prominent herbs were *Coptis trifolia*, *Matianthemum canadense*, *Lysimachia quadrifolia*, *Aster* spp., *Rubus triflorus*, *Clintonia borealis*, *Solidago* sp., *Cornus canadensis* and *Aralia nudicaulis*.

The lowest part of the woods lies somewhat north and east of the station. In early summer it comprises a swamp through which runs

a small stream. Here occur several forms not seen elsewhere. The most conspicuous are: *Fraxinus pennsylvanica* (a few young individuals), *Cornus stolonifera*, *Typha latifolia*, *Viola* sp., *Onoclea sensibilis*, *Ranunculus abortivus* and *Galium trifidum*.

Along the borders of the coniferous forest, especially towards the north, the following arborescent forms appear, all as young growth: *Amelanchier canadensis*, *Prunus pennsylvanica*, *Prunus virginiana*, *Prunus serotina*, *Populus grandidentata* and *Salix* sp.

It will be seen that many shrubs and herbs are species in general characteristic of northern coniferous forest. Some even appeared among the sub-dominants of alpine spruce-fir forest on Mount Ktaadn. The presence of several species, such as red clover, in this type of habitat can only be explained by the adjacent agricultural lands. To this extent is the forest atypical of untouched habitats of this type. It was, however, the only area available for study that even approximated natural conditions, and the interior region where the collecting was done, as contrasted with the borders, was less affected with these invaders and more nearly agreed with the original forest biota. The general appearance of the habitat is shown in Fig. 4. The interior of the forest, showing the deciduous undergrowth and giving some idea of the stratification of the plant societies, is shown.

The soil was examined by methods used in the examination of the Mount Ktaadn soils, which in turn were adaptations of the procedure of Adams (1920) in the examination of the Mount Marcy soils. Chemical and physical analyses were made, but the specific acidity was not taken. The sample was taken as follows: the pine needles and other forest floor trash were brushed away, and a hole was dug in the ground. A sample of the upper eight inches of soil was shaved off with a spade and placed in a can. The results of the analyses are given in tabular form (Table VII). It will be seen that this mainly a clay and silt soil, possessing much less sand than the least sandy of the mountain soils examined. Its nitrogen content is also higher than that of any of the soils examined for the mountain. Its acidity was much lower than any except the heath tundra. This soil was quite wet during the earlier part of the study, but in the latter part of the summer it became drier and friable, at least down to the depth (about 10 cm) which was examined for animal population. No doubt this was in part due to the rather scanty herbaceous cover over portions of the area examined.

The temperature was recorded by means of thermographs, and self-registering thermometers, the latter being read at critical periods, as will be seen later for the individual instruments. The self-registering maximum and minimum instruments were all checked by a standard instrument, and were in turn used for setting the thermographs. Throughout the

period of study temperature records were taken for soil, shrub and tree strata, and for a considerable period during the latter part of the study records were taken for the dead leaf stratum as well.

The instrument used for the measurement of soil temperature was a maximum and minimum thermometer, which had been corrected by comparison with a standard instrument. This was placed in the ground, just below the layer of dead pine needles and forest-floor debris. The exposure was made as follows: 1.5 m west of the lower instrument shelter (see below), in a plat shaded by young maples and balsam firs, a rectangular hole was dug, .4 m deep, .3 m long, and .2 m wide. This was lined, sides and bottom, with wire-screencloth on a frame, to keep out debris and to keep the sides from falling in. The whole was covered with a heavy grating of wooden bars, overlapping generously on all sides, which was laid on the ground to cover the opening. This grating was in turn covered with galvanized wire screen, on which was placed a mat of dead needles, organic trash from the forest floor, top soil and plants growing thereon, just as it was scraped up from the adjacent forest floor.

The whole was designed to make a chamber, in which instruments could be exposed, surrounded by the soil and covered by the dead leaf layer. The thermometer was exposed in this, a small hole being cut in the wire screen between two of the slats of the grating, through which the instrument could be drawn up, read, set and returned. At other times this opening was kept covered with a piece of bark.

Readings were taken twice daily, at 7 A M and at 7 P M with few breaks in this procedure. During the greater part of the study no attempt was made to take a set maximum (maximum reading immediately after setting), since this exposed the instrument so long to the air temperature that it tended to respond thereto, before it could be lowered into the observation cavity. The instrument, was, therefore, quickly withdrawn, read, set, and as quickly returned, usually before the air temperature had time to affect the mercury, and always before it had time to affect the indicator (reading). The results of the readings appear in tabular form (Table VIII) and in graphic form (Figs. 10 and 11, curve labelled C).

Temperatures of the leaf stratum were not taken until July 19. At that time a soil thermometer was exposed by being thrust 8 centimeters into the leaf and debris layer of the forest floor, in a spot shaded with young firs and birches (none over .8 m in height) 2.5 m east of the lower instrument shelter. It was thought that this would give a more reliable temperature for the leaf layer *on* the ground, than the thermometer exposed in the soil observation chamber *under* this dead leaf layer. The instrument was read twice daily, at 7 A M and at 7 P M, and during the latter part of the study an additional reading was taken in the early afternoon whenever possible.



The data so obtained are tabulated (Table IX) and shown as curve D in the plate and figures referred to above.

The air temperature at the level of the shrub stratum was taken by instruments exposed in an instrument-shelter of the standard Weather Bureau type, with louvred sides and slatted bottom, thus protecting the instruments from the direct effects of rainfall or sunshine, but permitting a free circulation of air around their sensitive elements. Throughout the study a United States Weather Bureau type maximum and minimum thermometer and a thermograph were left in this shelter, which was about .6 m above the ground on the north side of a large white pine. The thermograph placed here was frequently checked with the maximum and minimum thermometer, with which it was exposed. Its records were kept throughout the summer, but as its recording principle was somewhat defective, and it showed a consistent lag of at least two degrees, which could not be overcome by anything that could be done in the way of lightening the drag of the lever and increasing the air exposure of the responding metal parts, the records taken with it have not been included in the present report. In their place have been substituted records taken with the maximum and minimum thermometer.

This instrument, which from its accuracy was used in checking the others used in the study, was read as far as possible twice daily, at 7 A M and at 7 P M. During the latter part of the study another reading, in the early afternoon, was taken daily. The results appear in Table X and as curve A on the plate of temperature data cited above.

A thermograph was exposed in an instrument shelter, of the same type of construction as the one just described, which was suspended 11 m above the ground on the north side of a large pine, in a moderately thick growth of white and Norway pines (Fig. 4). While not at the top of the forest crown, this shelter was among the upper branches and far above the tops of the deciduous trees growing among the first growth conifers. The shelter was suspended by a rope and pulley from a protecting pent-house cover, and could be lowered to change the sheets and check the contained instruments, as was done every Monday and from time to time during the week. This thermograph was a very reliable instrument indeed, gave no mechanical difficulty and checked well, showing little or no lag, with the U. S. Weather Bureau type thermometer, when both were exposed to like conditions. From it was gained the data given in Table XI, and shown as curve B on Figures 10 and 11.

The record sheets on recording instruments were changed Monday morning. The method used in the translation of the recorded curve to figures of maxima, minima and means was a modification of that suggested by Weese. He estimated the mean temperature for each two-hour period on the ruled charts, and used the average of these means as the weekly

mean temperature. It was found by computing charts in this way and by the method of averaging the actual temperatures recorded at the end of each two hour interval that the results were practically identical over the period of a week, and inasmuch as this latter was somewhat of a time saver the method was adopted. Dr. M. S. Johnson, who suggested this method and has employed it himself, states that in all cases the results gained from computing charts by these two methods show insignificant differences, and this irrespective of whether the weekly fluctuations are great or small and the curves in consequence abrupt or smooth. For shorter periods no doubt the actual two-hours means would have to be computed. A base mean was computed in accordance with that used by Weese, that is the average for the week of the mean temperatures existing during the comparatively stable period of the day between 8 P M and 6 A M; this of course was not practicable for the simple instruments used, and was employed only in the case of the thermographs. Besides this the soil and leaf strata hardly show sufficiently marked fluctuations to make the attempt to determine a base or night mean of value, even had recording instruments been available.

For all stations absolute maxima and minima, mean maxima and minima, mean temperatures and extreme and mean ranges for each week of the study were computed; for the upper tree station was figured in addition the weekly base or night means and the deviations (mean) above them. The data is presented in Tables VIII, IX, X and XI, and in Figs. 10 and 11.

Since it has been seen that the soil temperatures show a marked lag behind the air temperatures, in their response to the general meteorological conditions, it will be best to take them up last. The air temperatures show two high points during the study, occurring during the weeks of July 14 and August 11, and were showing another marked upward tendency at the time the study was closed. The lower, earlier portions of the curves indicate the general rise of the spring temperatures up to the time of the July maximum; this is of course broken by minor fluctuations. The study was closed too early to show any traces of the autumnal fall. The actual fluctuations of the temperature as observed are probably not of any great significance; they do, however, show a considerable range of variability in the air temperatures of this habitat as a whole. If we consider now the stratal differences in temperature, we see that, while for a rather considerable period the temperature in the upper tree stratum is above that of the layer of air near the ground, especially during the middle and latter part of the study, still this is by no means always the case, nor as consistently the case as Weese found for similarly placed instruments in Illinois elm-maple forest. This may be explained by the position of the upper instrument which, while high

enough to be independent of ground and undergrowth influences, was not, because of the great height of the trees and the fact that their branches were thickest at the top, in the forest crown but below it, and hence covered by a heavy canopy of branches from the direct effects of the sun.

Of more interest in the present problem are the temperature relations of the layer of air just over the surface of the ground and those of the ground itself and the stratum of dead leaves that covers it. It is an axiom that soil temperatures in general and forest soil temperatures in particular, are more stable than the overlying atmospheric temperatures, and the causes are obvious (Adams, 1915). One of the factors in this phenomenon, the equalizing effect of the layer of forest-floor debris, is of interest in connection with the study made of temperatures found in this latter stratum. It will be seen that the temperature of this latter closely accompanies the soil temperature, but is, on the whole, more responsive to the general atmospheric temperature conditions, as might be expected, rising before the soil temperature in periods of rising temperatures and falling first during periods of falling temperatures. In general, our figures indicate a stratification of temperatures, with the steepest gradient between the leaf and shrub levels, whereas the two upper and the lower strata examined show temperatures accompanying each other more closely. All, however, show a fairly uniform agreement, maxima and minima developing together in the different strata with unimportant exceptions, and the temperature showing a general rise from the lowest to the highest strata.

If we now consider the temperature ranges in the different strata, we see a more complete stratification than is shown for weekly mean temperatures alone. The forest upper strata show a high degree of variation for a single week, and thence the index of variation decreases downward until we reach the soil, where the variations are smallest and the temperature relatively uniform. There is a well-marked difference in the extent of temperature variation between the tree and shrub strata, and some, but less conclusive evidence of stratification between the leaf and soil strata. But the great break, as in the actual mean temperature curves, lies between the leaf and shrub conditions. Here, as in deciduous forest "in summer the temperature increases from the soil upward to the forest crown; . . . . the temperature is most variable in the forest crown and least so in the soil" (Weese).

Humidity of the atmosphere was measured at the herb-shrub level and 11 m above the ground. The instrument used to measure the relative humidity of the lower strata was a hair-hygrometer which, after adjustment by a standard instrument, was exposed in the lower instrument shelter with the thermograph and maximum and minimum thermometer used for measuring the temperature of the lower air strata;

this shelter was in turn partly shaded by young maple and balsam fir. This hygrometer was used as the standard instrument, by which the hygrograph in the upper (11 m above ground) instrument shelter was set and checked. It was read twice daily, with a few exceptions, at 7 A.M. and at 7 P.M. During the latter part of the summer an additional reading was taken on most days early in the afternoon.

The only hygrograph (recording hair hygrometer) available for the study was exposed in the upper instrument shelter along with the thermograph used for recording temperature at that level (11 m above the ground, Fig. 4). It was a sensitive instrument, and checked well with the hair hygrometer used to set it, when both were exposed to the same conditions.

The tables (Table XII and XIII) and Figures 12 and 13 give the data obtained from these instruments, which was computed in a manner similar to that used for the computation of temperatures. Here, however, the base mean (Weese) is high instead of low, as the humidity almost always reached 100% sometime between the hours of 8 P M and 6 A M. Absolute maxima and minima, mean maxima and minima, mean relative humidity and total and mean ranges are tabulated for both stations; in addition the base mean for each week and the mean range below it are given for the upper station, where alone a recording instrument was available.

The curve of relative humidity of the herb-shrub stratum shows several high and low points which are not correlated with temperature differences, as far as can be seen. Neither are the extreme differences shown (18% of relative humidity) sufficient to be of any marked significance, since the fluctuations of a single day may reach a figure of 69% at the same station. The curve of mean relative humidity for the tree stratum is consistently lower, with a single exception, than that at herb-shrub level. This is the usual condition, because at the lower station the moisture-laden atmosphere in contact with the more or less damp forest-floor, is less rapidly removed by air currents and its place taken by the drier air coming from over adjacent cleared land. The average difference between these two stations for the period studied was 7.5% relative humidity, as compared with the figure 3.5% given by Weese for deciduous forest. The discrepancy is no doubt due to the fact that the present study was made entirely in the summer, when such differences are at their greatest. While the study of deciduous forest conditions by Weese embraced a complete annual cycle, his humidity data for the tree stratum were not taken during the early part of the summer.

The curves of mean ranges for the two stations (Fig. 13), show a condition of large variation, both relative and actual. Particularly is this true of the tree stratum. This agrees perfectly with the finding given

for deciduous forest that between the herb and shrub strata on the one hand and the tree stratum on the other there is "almost invariably greater mean relative humidity in the former situation and a greater mean daily range in the latter" (Weese). The most casual glance at the curves shows that this might have been as well said for the conditions of relative humidity stratification found by the writer. The mean daily range curves are entirely distinct throughout.

It will be seen that the upper strata of the forest air are regions of lower relative humidity and more marked fluctuations in this factor whereas the lower strata, adjacent to the ground, are regions of somewhat higher relative humidity and immensely greater stability. The significance of these factors and their effect on the animals will be discussed in due course.

Since the evaporating power of air has generally come to be considered as the most reliable general index of all the other physical factors which affect organisms of terrestrial habitats, an attempt was made to measure this factor in the coniferous forest area studied, especially in its relation of stratification. The instruments used were Livingston porous-cup atmometers of the spherical type, which were exposed at nine stations at various localities and strata of the forest habitat. Of these, the records of one instrument, a black atmometer exposed with a white one for measurement of light effects, have not been included, since there was no other similar instrument with which to compare it.

The instruments employed were new and standardized cups direct from the makers. They were restandardized at the close of the study, but were not standardized during the study, of which the actual duration was about nine weeks. For comparison with each other, the readings taken each week were changed by a coefficient to those of a standard instrument.

For field use the atmometer cups were mounted on quart bottles by the simplified non-absorbing mounting described by Livingston and Thone (1920). The weekly filling was done Monday, by means of a burette, the bottles being filled to a file-mark on the neck of the reservoir bottle. As indicated by the results, the quart bottles were larger than needed for weekly studies in this climate and habitat; for field-work in northeastern (or probably northern) coniferous forest, a pint bottle would be sufficiently large, and would practically halve the amount of distilled water that must be carried.

The exposure of atmometers was as follows:

No. 1, Black spherical atmometer exposed one meter above ground, and 2 meters from the lower instrument shelter, under the leafy branches of a young maple.

No. 2, White spherical atmometer exposed 1 meter above ground with No. 1.

No. 3, White spherical atmometer exposed near surface of ground (0.3 meter above surface) near Nos. 1 and 2 and, save for height, under identical conditions.

No. 4, White spherical atmometer 2.5 meters above ground, in cylindrical basket of galvanized wire hanging from lower limb of small hemlock 4 meters northeast of the lower instrument shelter.

No. 5, White spherical atmometer exposed with the maximum and minimum thermometer in the observation chamber in the soil already described; the sphere was just beneath the grating, covered with the usual layer of pine needles and other forest-floor debris.

No. 6, White spherical atmometer exposed for two weeks at the beginning of the study on the ground among high grasses in a swampy glade on the eastern edge of the forest. There was no forest cover, in the ordinary sense of the word, although the glade was surrounded by a dense growth of high bushes, so that there was little wind, although the sun shone there brightly during most of the day.

No. 7, White spherical atmometer exposed 6.5 meters above the ground in cylindrical basket of galvanized wire suspended from the upper instrument shelter on north side of large pine tree (Fig. 4, about the middle of the picture).

No. 8, White spherical atmometer exposed 11 meters above the ground, in bracket attached to side of upper instrument shelter (Fig. 4).

No. 9, White spherical atmometer (same instrument as No. 6) exposed from July 7 in a position among grass and herbage on the western edge of the forest, where the latter meets a wide area of grassland. Here it remained until August 4, when it was destroyed by children.

The results of the entire series of observations are given in tabular form (Table XIV) and shown graphically. Figure 14 shows the curves of evaporation by stations, through the period of the study and Figure 15 the mean amount of weekly evaporation from each instrument for the entire period.

The curve of evaporation from the atmometers directly exposed to the air showed a general increase for the first three weeks of observation, thus reaching a high level which it maintained, with slight up and down fluctuations, for the next month. At the end of that period, evaporation in all forest stations decreased sharply, the most marked change taking place in the upper stations and thence decreasing gradually towards the ground stratum. Following two weeks of this decrease, the second week more gradual, the trend of evaporation again turned upward, and rather sharply, for the final week of observation. The earlier changes appear to be some degree independent of the amount of rainfall during the weeks when they occurred; thus the evaporation of the first three weeks mounted steadily, in the face of a decreasing precipitation, perhaps assisted by

the moderate rise of temperature during the same period. Also the high rate of evaporation maintained during the next four weeks accompanied a generally decreasing rainfall, the highest point reached on the week of August 4 following a period of two weeks when the precipitation was very light indeed. Following this, however, the evaporation fell off rapidly, as has been seen, and did not rise again until considerable precipitation had occurred. From these things we might infer that the conditions of coniferous forest are such as to cause a moisture retention, a reservoir, as it were, of the abundant precipitation of the winter and spring months; from this supply of moisture, evaporation increases, in part due to increasing summer temperatures, until the latter part of the summer, when evaporation falls off unless the moisture of the forest habitat is restored by further precipitation. In this connection it may be said that the condition of the soil and pine needles layer of the forest lower strata, as observed for moisture during the period of the study, exactly bore out this conception.

Of the various physical factors thus far considered, the evaporating power of the air shows the most complete evidence of stratification (Figs. 14, 15). It will be seen that none of the station evaporation curves overlap at any portion of their extent. It appears that the evaporating power of the air, as found in this habitat, shows two large breaks with steep gradients in stratification, one between the ground and leaf strata on the one hand and the herb stratum on the other; and one between upper shrub or high bush stratum and the tree station, low and high, proper. This will be most apparent if Figure 15 is examined without regard to columns 6 and 9, which represent evaporation at stations outside the forest proper, but it is also indicated in Figure 14. In other words, going from the floor of the forest upwards, we have first, under the leaf layer on the forest floor, a condition of very low evaporation; thence we pass, by the steepest gradient in the series, to the group of stations represented by Nos. 3, 2 and 4, which form a group of herb, shrub and high bush strata, between which the gradients are of the same order; above this is another steep gradient, separating stations No. 4 and No. 7; both these last constitute a group of tree strata proper, and between the two the gradient is again "easy." The cause of the first and sharpest cleavage will be evident at a glance; the cause of the second is suggested by looking at Fig. 4. It represents the crowns of the lower-growing deciduous underwood of the much higher coniferous forest.

If we take as a standard atmometer No. 2, 1 m above the surface of the ground, we see that there is a constantly lower evaporation here than in the tree 1.5 m above, and that the differences between the two levels are moderate in amount, and both actually and relatively higher with periods of high evaporation. The relative evaporation from these

two levels does not show the relations with precipitation for the period found by Weese for corresponding stations in elm-maple forest; so far so far as can be seen, the points of greatest difference between the evaporation at the two levels fall on weeks showing widely varying degrees of precipitation.

The evaporation from instrument No. 7, 6.5 m above the ground shows, as we have seen, a sharp and constant difference from that of No. 4 just discussed. This instrument was well above the tops of the deciduous underwood, and therefore might be expected to show evaporation of a different order of magnitude from that shown by all the instruments below their level. Not only is this found to be true, but its curve never even approaches that of the next lower stratum (No. 4) except at the time of lowest evaporation, and then not closely.

The maximum evaporation was that for instrument No. 8, exposed 11 m above ground. This followed throughout, however, the type of curve followed by the other instruments exposed directly to the air. It is of the same order of magnitude, as far as its weekly means of evaporation are concerned, as the 6.5 m instrument just below it (No. 7). The reason for this has already been discussed. It should be remembered in this connection, however, that the 11 m instrument was by no means at the forest top; an instrument placed there would have added at least a minor and perhaps a major evaporation stratum to those already discussed.

Turning now to the instruments which were exposed below the 1 m level, we see that atmometer No. 3, 0.3 m above the ground, showed a constant and definite curve lower than that of the 1 m instrument (No. 2), and following it within expected ranges throughout the study; this instrument shows one break in the record, occurring for the week of August 4. While this curve is constantly lower than the curve of the instrument next above it, it will be seen that the differences are moderate in amount, and that the evaporation differences are of the same order. The constancy of the differences, however, is of interest.

The most extreme results in the direction of small evaporation were obtained in the case of the instrument which was exposed in the observation chamber under the artificial mat of pine needles and debris. This instrument may be supposed to have given some idea of the amount of evaporation occurring from the top soil through the dead leaf stratum. It will be seen that the value is very low throughout the study, never exceeding a single cc and sometimes falling to almost nothing, although a measurable evaporation was always present. Still more interesting is the extent to which the extremely low curve agreed, in its weekly fluctuations, with the curves of the instruments exposed directly to the air in the strata above ground. It is interesting that the atmometer should be found



sufficiently sensitive to respond to differences communicated to it through a three-inch layer of forest-floor debris. The average weekly difference between the evaporation here and in the first (0.3 m) level above the ground is practically 8 cc for the habitat studied, the greatest found between the evaporating powers of any two adjacent strata.

The curves for evaporation at the forest-edge stations have not been given. The weekly mean of evaporation for the period over which they were studied is illustrated graphically in Fig. 15 where the columns representing these two stations are placed in the general series of forest stations, in the order to which their magnitude entitles them. If we examine column 6, the record for a swampy open glade outside the forest on the east, we see that it possesses the lowest evaporation value of that found for any station except the sub-leaf one. Here, in an open but swampy glade, surrounded by high grass, and cut off by surrounding bushes and by the forest itself from wind, and especially from the prevailing fair and drying westerlies, evaporation is even lower than anywhere above ground in the forest.

On the other hand, column 9, representing the mean weekly evaporation for an instrument exposed among grass and herbage on the western forest margin, and just at the edge of wide tracts of grassland, showed an evaporation higher than that observed anywhere in the forest below the upper strata. The influence of wind is no doubt preeminent here. The differences between these two forest margin stations indicate that conditions at this tension zone may be very different under different local conditions—more so, in fact, than stratal differences within the forest itself.

Considering further Fig. 15 it will be seen that the actual order of increase in evaporation, beginning at the lowest, as seen in the entire series of observations is: sub-leaf stratum, swampy forest-margin, herb stratum, shrub stratum, high bush stratum, dry forest margin, low tree stratum, high tree stratum. The actual figures of mean daily evaporation, as expressed in this order, are:

Station	5	*6	3	2	4	*9	7	8
Height								
in m.	-.08	0.3	0.3	1.0	2.5	0.3	6.5	11.0
Mean wk.								
evap. co.	0.2	6.2	8.2	11.2	14.0	17.4	19.7	21.0

Speaking of deciduous forest, Weese (1924) says: "The gradient in the evaporating power of air in the forest is very striking,—stations, less than a meter apart, vertically, showing definite and constant differ-

\*Forest margins.

ences. This is particularly true at the lower levels. At the higher levels the gradient still persists but is subject to irregularities due to the greater exposure and lack of uniform conditions." All this equally true for coniferous forest, and even more regular and constant. The absence of seasonal changes in vegetation of the upper strata would tend to obviate some of the interlocking of the upper strata curves found by him as coming about the time of the leaf-fall. The relative seasonal differences of the evaporating power of air in coniferous forest might be as marked for spring, fall and summer, as those found by him in deciduous forest, especially in forests where there is an abundant herb, shrub and low tree strata of deciduous plants.

Here, rather than at the forest crown of coniferous forests, should we expect to find at critical seasons the stratal irregularities in evaporation most marked; probably even here conditions would always be stable as compared with those in deciduous forest, where the entire forest cover is shed in the fall, since the cover of the conifers would have a stabilizing effect. This has not been studied.

The only apparatus available for measuring the light in the present study was a Wynne exposure meter, the ordinary photographic apparatus of the sensitized-paper type; this was employed to get some idea of the relative light intensity under different conditions in the forest environment. This of course measures the actinic rays only (Shelford, 1912); it has been pronounced fairly satisfactory for that purpose (Bates and Zon, 1922), and was the only type of illuminometer available. Regular readings were not begun until the early part of August, and some of the first ones taken showed so wide a range of variation, under what appeared to be very similar conditions of light, cover, etc., that they were discarded. However, it finally seemed best to take what readings were possible, in the hope that by averaging a number of these, some idea of the relative light intensity at the different stratal levels might be obtained.

The readings were mostly taken in the early afternoon, and within as short a time as possible of one another; perhaps the average interval between readings may have been three minutes. The same sensitized sheet was used for all readings taken on a given day, to obviate any inaccuracy arising from the comparative freshness of the paper or the reverse. The darker of the two standard tints was the one used in matching, because, while this took longer to match in the darker localities, it was the only one which could be used with any accuracy in the stronger light, where the lighter tint was so soon matched that it was impossible to obtain even approximate accuracy. A stop-watch was used, and the readings as given are in seconds.

A record was made of the general weather conditions at the time of each reading, as far as they could be described by the observer. In

the longer readings the amount of light changed perceptibly during the time taken to match the colors; this is indicated on the records under remarks on weather conditions.

The readings were taken from the same stations throughout the study, which may be described as follows:

**On the Ground:** The place was five meters east of the lower instrument shelter, in a spot covered with the typical amount of shade from young saplings (beaked hazel, ash and alder) and, of course the conifers. The forest crown begins about 5 m from the ground in this place, and becomes thicker higher up, but always is of a rather open character. The data from this station are given in Table XV.

**Above the Ground, 1.5 m.** The actual locality was the same as for the ground reading, save for the elevation. The instrument was shaded by a growth of young maple. The data are given in Table XVI.

**In Open Glade:** 25 m north of the tree bearing the upper instrument shelter. This place was covered by a forest-crown shade almost, if not quite, as dense as that for the two previous stations, but was characterized by the almost total absence, over an area about 30 m square, of the growth of shrubs and young deciduous trees, especially maples, which was characteristic of them. (Fig. 4, right foreground). The data are presented in Table XVII.

**In Open Grassland:** 20 m from the western edge of the forest. This reading was taken in an attempt to get some idea of light intensity in the absence of forest cover, and hence the illumination of the forest crown, where it was impossible, for obvious reasons, to take actual measurements. The data taken at this station are shown in Table XVIII.

Considering this data, it appears that there is a very definite stratification of light in the coniferous forest habitat and that the light available in the lowest strata is a very small fraction of what is available higher up. In fact the imperfections of the method, especially of measuring the strongest light, probably make this fraction appear much larger than it actually is. It is interesting that the steepest light gradient should exist between the ground and the next stratum measured above it, a condition of things comparable to the position found for the steepest gradients of temperature, humidity and evaporating power of air. The relation between the light intensities in the glade and in the open tend in a general way to support the statement of Weese for deciduous forest, that the light which enters into large openings in the forest is little lessened in its intensity. Considering the reading made in the shaded but rather open glade, it is evident that the light there is a considerable fraction of that found in the grassland outside, whereas the light on the shaded forest or even above it under the shade of shrubs and small trees, is a very small fraction. The method employed was too rough to make these actual

figures of significance, either by themselves or for comparison with those taken with more elaborate instruments in other habitats, but the data indicate the fact, direction and to some degree the extent, of light stratification in the forest environment.

#### THE BIOTA

In studying the animals of the coniferous forest tract, and especially their stratification into societies, the methods of Weese (1924) were largely employed. The collections were taken most frequently during the latter part of the study; therefore the biotic data for the month of August is the most complete. Collections were made according to the quasi-quantitative method of sampling from the various strata, in the immediate vicinity of the stations where the instruments were exposed. Four strata were studied systematically, the soil, dead-leaf, herb and shrub; the tree stratum being neglected in the present study. On each date when collecting was done, these four strata were "sampled." The dates given are those on the last day of the week when the samples were taken, thus corresponding with the instrumental observations, which are dated on the day they closed. In a few instances during the latter part of the season additional collections were taken in the middle of the week. The animals from the different strata were collected as follows: Weese's original paper should be consulted for further details, as the writer closely followed his practice, in order that the data from the two habitats might be to some extent comparable.

Soil collections were taken from the upper 10 cm of soil, from which the leaf cover had been previously removed. The soil was explored over an area 2 ft square, being carefully dug over with a trowel to the depth of 10 cm. Whatever animals were found in this plot were placed in vials.

Leaf collections were made from the layer of dead leaves (largely pine needles) and other organic matter which covers the soil. This layer was swept up from the previously measured 2 ft quadrat, placed quickly in a cage-box made of very fine mesh wire-screening, and carried to the laboratory, where it was treated with ether and examined for its animal population.

Herb collections were made by ten sweeps of an insect-net with a 30 cm mouth over and among the plants of this stratum.

Shrub collections were taken in the same way at the higher level; paper bags were used for carrying the last two samples to the laboratory.

The quantitative results of these collections appear in Table XIX and in the form of a graph (Fig. 16). The latter gives by curves the total and stratal populations.

The curve of total population (A) is seen to be a very irregular one. Starting with a medium position for July 7 it falls steadily through July 14

to July 21, and then takes a sharp upward trend for the week following. By August 11, when the next collection was taken, the population had again fallen, and it continued to fall, reaching by the middle of the following week the lowest point observed during the study. By the end of the week it had again mounted abruptly, but suffered another fall during the middle of the week of August 25. But by the end of that week it had mounted to the highest point reached at all, whence it declined somewhat to the last collection which was still, however, above the average. The peaks of this curve all fall in periods of relatively low temperature, but this is probably not significant, although Sanders and Shelford (1922) found high temperatures accompanied increased animal population in a pine-dune animal associates, while Weese finds high temperatures in elm-maple forest conducive to low animal populations. It is unlikely that the animals of cool, moist coniferous forest would be restricted in numbers by temperatures no lower than the lowest of those recorded. Entirely similar types, inhabiting the still cooler alpine spruce-fir forests of Mount Ktaadn appear to be independent of much greater temperature extremes than this, in all matters save that of a daily rhythm of activity. The marked high points on the curve appear to be largely due to the presence of certain particular species whose numbers attained a maximum, rather than to any general increase in the numbers of any considerable number of the species making up the population. Thus one of the highest points is produced by the large numbers of Chironomidae taken on July 28.

If we consider now the size of the various stratal populations, we see at once that the shrub stratum contains the largest and also the most fluctuating animal population. This condition is the reverse of what has been described for deciduous forest by Weese, where the population of the herb stratum is uniformly larger than that of the shrub stratum. An examination of the curves given in Fig. 16 shows that for the area and season studied the numbers of shrub animals were rarely below, and often much above, the numbers of herb animals. The shrub stratum in fact to a large degree controlled the general population curve, especially in its extremes. This is probably in part due to the scanty herb cover in the coniferous forest habitat. The first of the two marked maxima shown by the shrub curve was, as has been said, caused by Chironomids; the second, that of August 25, was due to several species of Hemiptera and Homoptera.

The herb stratum was second in size and rather uniform, though presenting some fluctuations in numbers during the latter part of the season. These maxima were caused by several species of insects and young spiders, which will be taken up in more detail under the study of individual species in their relation to the stratal societies.

The population of the dead-leaf ground stratum was considerably lower, on the average, than that of the herb stratum, and might have been expected to have been lower still in comparison. No doubt this was influenced by the relatively low numerical value of the herb stratum in this habitat, as compared with the same society in deciduous forest. The soil stratum was of low value throughout, but very uniform. Its population is largely a resident one, as far as the dominant animals are concerned.

The entire animal population as collected is given numerically in Table XIX.

With a few exceptions only the predominant animals of the various strata will be discussed, present in such numbers, as compared to the other species, as to play an important part in the community. Certain animals were very scarce or wanting; only a single mollusk was taken during the entire season, *Phylomycus carolinensis* (Bosc), on August 22; the coniferous forest habitat is poor in this group (Walker, 1906).

The birds of the area were not studied. An attempt was made to get at the size and composition of the mammalian population by extensive trapping during the latter part of the season. The results of this were somewhat surprising. Only two species of mammals were trapped and one of these, the shrew *Sorex personatus*, was rare. The other, the short-tailed shrew *Blarina brevicauda talpoides*, was very abundant. In all the trapping done not a single specimen of the white-footed mouse, jumping-mouse or short-tailed meadow mouse was taken, although the first might have been confidently expected throughout the habitat, and the last in the grassy regions abutting on the swampy eastern area. It was not possible, because of lack of time, to investigate other territory in order to find out whether the scarcity of usually common animals was general in the vicinity. The area studied was not far from the college poultry-plant, and there were outlying chicken-pens within a few hundred yards. For this reason, there was always a number of smaller carnivores hanging around this forest tract, especially skunks and half-wild cats. It is possible that this fact may have had something to do with the absence of mice through the area studied; whether or not carnivorous animals show any preference to mice, as contrasted with the pugnacious and rank-fleshed shrews, is not known. The latter are certainly sometimes eaten. The red squirrel was the only other mammal noted.

If the general population curve (Fig. 16) is inspected, and still more if the curves representing the seasonal abundance of dominant species are examined (Figs. 17-20), it will be seen that the greater part of the study fell between the period of the high vernal rise in population and the later aestival rise, including only a little of the last part of the former but largely covering the latter. Further, if we omit from consideration forms

not strictly belonging to the forest habitat as such but incidental on the presence of nearby aquatic habitats, especially the chironomids, we see that this relation becomes even more apparent. The study did not last sufficiently long to show the entire march of the summer societies, but it indicates some of the phases of the series. Since the only well-developed seasonal society occurring in the study was the aestival, the dominants of that alone will be discussed in detail. These fall into well-defined stratal societies. Listed in order of abundance they are:

#### CLASTOPTERA (SHRUB) SOCIETY

Subinfluent: *Clastoptera obtusa* (Say), *Tetragnatha* sp. (juvenile), *Graphocephala coccinea* (Forst.), *Macrosiphum coryli* Davis, *Philodromus* sp., *Diaphnidia pellucida* Uhl.

#### LEIOBUNUM (HERB) SOCIETY

Predominants: *Chironomus dispar* Meig., *Chironomus modestus* Say, *Leiobunum politum* Weed, *Chironomus decorus* Johann., *Tanytus melanops* Meig.

Subinfluent: *Dicyphus famelicus* (Uhl.), *Nabis* sp. (juvenile).

#### TOMOCERUS (LEAF) SOCIETY

Subinfluent: *Tomocerus flavescens* Tullberg var. *separatus* Folsom, *Linyphia* sp. (juvenile).

#### HELODRILUS (SOIL) SOCIETY

Subinfluent: *Helodrilus caliginosus trapezoides* (Dugés).

It will be seen that the predominants are mostly arthropods. Mollusks were, as has been seen, almost wanting. Among the insects, only a few species of Lepidoptera and Hymenoptera had been determined when the study was completed; these orders may have contained predominant species. The same is true for certain dipterous larvae and for various myriapods, some of which were quite numerous in the lowest strata. It is interesting to note that no Coleoptera appeared among the dominants, and that this order was in general poorly represented; this a group which Weese found to be decidedly predominant in elm-maple forest. Here their place seemed taken by ecologically equivalent phytophagous Hemiptera.

Figs. 17-20 give the observed seasonal and stratal (for some species) distribution of the more important predominants. The curves of distribution through the season are in some instances separated to show the stratal occurrence of the species in different stratal societies, such curves being separated and placed one over the other. The time is the same for all the figures and agrees with the scheme used for the presentation

of temperature and humidity data (Figs. 10-13). The increments used in plotting the heights of the curves may be different for different species, and the polygons have been smoothed.

#### Clastoptera (Shrub) Society

*Clastoptera obtusa* (Say) Fig. 19, Aa and b.

According to Osborn (1916) the alder spittle-insect, under Maine conditions, hatches in late spring or early summer (July) and is common in the adult condition until early August, appearing afterwards, however, until September. It did not appear in the collections until August, when it suddenly appeared and thence its total population mounted until the close of the study. Its stratal distribution showed a marked downward movement for the middle of the weeks of August 18 and August 25, the numbers of animals decreasing in the shrub and increasing in the herbstrata. It will be noted that this is accompanied by a period of falling temperatures. This was also a period of falling evaporation. With rising temperatures and rising evaporation the herb population fell to nil, and the largest number of this species recorded for the study appeared in the shrub stratum about the first of September. This insect is said by Osborn to pass the winter in the egg stage; whether or not the sudden appearance of the adults in numbers so late in the season was an inward forest migration, similar to that observed by Weese for many beetles, cannot be definitely stated. The facts suggest it, but since this animal does not hibernate in the adult stage they are less conclusive in this instance.

*Tetragnatha* sp. (juvenile) Fig. 18, c.

These spiders were all young, which were abundant in the shrub stratum, during the latter part of the summer, preying on the smaller insects. They were not taken until the later part of the study and thence were present in slightly varying numbers throughout the remainder of the season, being sometimes taken in the herb stratum. Their maximum as adults comes earlier in the summer, before the greater part of the collecting was done, and they winter as young in the forest floor (Emerton).

*Graphocephala coccinea* (Forst.) Fig. 19, Ba and b.

This widely distributed leaf-hopper occurred in collections taken throughout the study. From the records of its occurrence in Maine, summarized by Osborn (1915), it appears to be generally characteristic of the late summer animal society, no records being cited earlier than August. It is characteristic of the moist forest habitat and occurs generally there on the herbs (especially ferns) and shrubs, etc.; it has been taken from the spruce-fir forest of Mount Ktaadn, no doubt from deciduous herbs and underwood. In the present study the animal was distinctly more a shrub species, although a constant smaller herb population existed



until the end of the collections, when the species disappeared from this stratum. There was a gradual increase in the total numbers, the species maximum being reached about the middle of August. As in the case of the alder spittle insect (*Clastoptera obtusa* Say) there appeared to be a response to the falling temperatures about August 18, the numbers of individuals falling off in the shrub and increasing in the herb strata, thus indicating a downward movement of the animals with the descending temperature.

*Macrosiphum coryli* Davis. Fig. 20, A.

This aphid is one of the few dominants which show the peak of abundance as occurring in the early part of the period of study. From thence it fell off gradually, but was present in varying but smaller numbers throughout the remainder of the time. It was principally a shrub-society animal, but sometimes occurred at the herb level, and a single specimen was taken from the leaf layer—no doubt fortuitously. Adults and young were taken on various dates during the entire period when collecting was done.

*Philodromus* sp. (juvenile).

The young of this crab-spider (probably representing several species) were found at the same levels frequented by the adults earlier in the season, in low shrubs within two or three feet of the ground. They were occasionally taken from the herb stratum lower down, where they did not occur as predominants. Like the other young spiders they reached their maximum of abundance during the month of August.

*Diaphnidia pellucida* Uhl. Fig. 20, D.

This mirid, like most of the other dominant insects, had an aestival maximum, occurring in the early part of August, at which time it appeared suddenly in the collections. Thence it decreased rapidly in numbers, none being taken after August 25. It was sometimes taken from the lower (herb) strata, but was principally a shrub animal.

#### Leiobunum (Herb) Society)

*Chironomus dispar* Meig.

This species was the predominant animal in numbers, but a species locally present, due to the damp habitat and aquatic and semiaquatic conditions found on the eastern border of the area studied. From the numbers, however, and the fact that it is often found in such coniferous forest stations, it seemed best to consider it among the list of predominants, with the above explanation. Considering the population as a whole, the peak of the midges appeared in the first collections, and after that there was a marked fall in numbers, followed by a second rise the latter part of the month of July; from this the curve fell again abruptly, to rise somewhat in the early part of August, but not attaining another high point

during the period of the study. This group, then, did not take part in the late August population increase, but shows, like *Macrosiphum*, the last of a vernal maximum, and an additional mid-summer maximum besides. It is largely to this fact that we get the high point on July 28 in the general population curve, the contributing factor being a large number of Chironomids of several species taken on that date.

If now the particular species *Chironomus dispar* Meig. is considered, it appears that this species, while taking part in the vernal maximum of July 7, did not attain its second maximum until August 4, or a week after the general high point for the family. Between these two dates lies a period of lower numbers, caused by the sudden decrease from the July 7 maximum and the gradual increase to the early August maximum; after the last date the population of this species again falls, but some individuals were present up to the end of the period of study. The decrease, sharp in both cases, does not appear to be connected with temperature or evaporation.

*Chironomus modestus* Say

This midge, as far as our collections indicate, did not take part in the general maximum of population observed for the family on July 7, but its midsummer maximum coincided with and increased the family maximum of July 28. Thence its decrease was even more rapid than that of *Chironomus dispar*, and its numbers were relatively less throughout the remaining period of study.

*Leiobunum politum* Weed. Fig. 18, a.

This harvestman, which was mainly a herb species, though rarely taken from the strata above and below, appeared in the collections towards the latter part of July, reaching its seasonal maximum the week of the twenty-eighth and after a slight decrease reaching another but lower summit the week of August 18. Thence the fall in numbers was rapid until the very end of the study, when a slight increase came, accompanying rising temperatures and evaporation.

*Dicyphus famelicus* (Uhl.) Fig. 20, Ca and b.

This mirid was one contributing to the general aestival maximum. It appeared the latter part of July, and thence increased steadily in numbers until the week of August 25, when its maximum was reached; its numbers had declined abruptly a week later, when the last collection was taken. It was distinctly a herb stratal dominant, but at the summit of its abundance it appeared also in smaller numbers in the shrub stratum (C-a.). It feeds on *Rubus* (Britton, 1923), of which the herbaceous form *triflorus* was found here.

*Nabis* sp. (juvenile). Fig. 20, B

Nymphs of this genus were present in small numbers throughout the period of collecting, but reached a maximum about August 25, after

which they took part in the general decline of the following week. They were most abundant on the herb stratum, but were taken from the shrubs from time to time.

*Chironomus decorus* Johann.

This midge is included in its seasonal occurrence with the general population of Chironomidae. The general remarks about the family as a whole apply to it, as far as its seasonal and stratal distribution are concerned.

*Tanypus melanops* Meig.

The same is true in general, for this species, as was stated for *Chironomus decorus* and for the family as a whole.

Tomocerus (Leaf) Society

*Tomocerus flavescens* Tullberg var. *separatus* Folsom. Fig. 17, b, c and d.

This spring-tail, the only species found in much collecting in the habitat, is a permanent resident and a numerical predominant of the dead-leaf stratum during the summer months. It is, however, sometimes found in small numbers in the ground (d), more rarely on the herb stratum (b). From its numbers it undoubtedly must work considerable change on the layer of decaying plant matter which makes up its real habitat. The fact that it was not taken in the first few collections was probably due to the fortuitous selection of an area where these animals were not found, such, for instance, as a very dry area. The maximum occurred on July 28; the following decline throughout the greater part of the collecting period is perhaps correlated with the gradual drying out of the leaf stratum, accompanied (d) by a partial migration into the soil, although the data is too scanty to more than suggest this. A very small rise in numbers came towards the very end of the study.

*Linyphia* sp. (juvenile). Fig. 18, b.

The population of young linyphiids showed in general the same course as the curve of the young epeirids, save that it developed more gradually despite its earlier start. The species first appeared early in July as straggling individuals, and gradually increased to a maximum the twenty-fifth of August, coinciding with the second maximum of the young *Tetragnathas*. There was a decrease and the evidence of a following increase towards the very end of the study. These were all young animals which would hibernate in the leaf litter. The maximum for the adults comes earlier, and the animals themselves are found in various situations higher up.

Helodrilus (Soil) Society

This was in general rather scantily populated for the period of study, and only a single predominant, a permanent resident, will be considered.

*Helodrilus caliginosus trapezoides* (Dugès) Fig. 17, A.

The presence of this lumbricid is in itself an indication that the station studied is not wholly typical of coniferous forest, but has had its animal population modified by neighboring agricultural lands. The writer has never taken it in the primitive coniferous forest around Mount Ktaadn, and in general such forests are poor in Lumbricidae. It was thought of interest to trace the numerical fluctuations of this resident soil animal, in order to see to what degree they could be correlated with various physical changes. The curve includes both adults and juveniles, but more of the latter, since the method of collecting favored the escape of the adults.

The first high point of the curve was that of the first date of collection, July 7. There had been previous rain, and the soil was wet, while the general condition of the forest floor was damp. Evaporation from the upper leaf strata continued rapidly and remained high for a period of weeks, during which the leaf and upper soil strata dried out appreciably; during this time the earthworm population of the upper soil, as judged by this single species, fell off as the animals retired deeper and out of reach of the collecting methods used. There was a slight increase July 21, correlated with the heavy rain of the period. The second and third apices correspond with the rainy weeks towards the end of the period of study, the difference between the two being probably unimportant, and due to the small local population of the quadrat selected for the second of these collections.

#### DISCUSSION

The coniferous forest habitat studied is a biotic environment of marked stratal differences in physical factors. These factors, in general, present a graded series from forest soil to forest crown, but the various strata fall into groups similar in conditions. These groups are: first, top soil and dead leaf strata; second herb, shrub, and high bush strata; third, low tree and high tree strata. The grouping is shown most clearly for evaporation. Since this is in itself a fairly reliable index of other physical factors and since the evidence from data on temperature and humidity tends, as far as it goes, in the same direction, we may assume that grouping with steep gradients between is the general condition. The strata, divided on a basis of the physical conditions, fall into "groups subordinate to groups." This is a suggestion of what has been pointed out, based on animal societies, for tropical forests by Brehm (1896).

The cover of tall conifers is a dominant influence through the entire association. Even more important in any single member of the series are the stratal societies peculiar to each layer. These determine more immediately the physical and biotic conditions under which animals live. This point will be considered further in speaking of animal response.

If we consider these strata in order from below upwards, we find that the upper soil stratum presents an environment of comparatively low but very uniform temperatures, minimum evaporation and minimum light. The animals inhabiting this stratum as more or less permanent residents are those whose reactions—and to some extent structure—are such as to find optimum conditions here: earthworms, the sparse mollusk population, ground and fungus beetles, and the larvae of a considerable number of other beetles and flies.

In the next layer above, the leaf layer, conditions are somewhat less equable. Our only instrumental data are for temperature, which is higher and more extreme than in the soil. Light is somewhat greater, undoubtedly, and moisture less. The differences in animal population between the two are very considerable, both for quality and quantity, nor are the animals common to both as numerous as we should expect. The few individuals listed as found both in the ground and in the strata above the leaf must be considered either wholly exceptional, as in the case of *Tomocerus flavescens*, or caused by the presence of animals, such as the spiders, whose adult and juvenile stages are passed in different strata. The real population of the leaf stratum seems out of all proportion to the physical differences between it and the upper soil. Conspicuous is the predominance of many young spiders during August, while the maximum of corresponding adult forms comes earlier and at upper strata.

All the data available on the physical factors agree that between this leaf stratum and the herb stratum next above it occur the steepest gradients in the series for temperature, evaporation and probably light. Both temperature and evaporation show not only a great rise but also a very marked increase in extent of fluctuation. An animal moving from one of these strata to the other certainly undergoes a very considerable change in its physical environment. The number of species making this change is comparatively small. Further, such are again largely species of spiders, whose adults habitually occupy the upper strata, and whose young were taken at all stages of their downward migration toward winter quarters in the forest floor. A very few species may be noted which seem to change strata rather indifferently at the adult stage; an example is *Camponotus herculeanus*. The population of the herb stratum proper is large, and more varied than that of any other single stratum analyzed. Predominant groups of animals present were mirids, cicadellids, and various families of Diptera.

The physical differences between the herb and shrub, while constant and by no means to be disregarded, appear to be of much less magnitude than those existing between the last two strata considered. They are, however, in the same direction, involving increase of evaporation and light, and a corresponding increase of the fluctuations of these, and

probably other factors not measured. In other words, differences between physical conditions at herb and shrub levels are less decisive than those previously discussed. This is indicated not only by the instrumental data, but even more by the animal population data. A large number of animals are common to both strata. Among them are several of the predominants. The animals found in the present study only at shrub level constitute a varied list; the predominants are several species of Diptera, although no single species appears particularly prominent; the same status may be accorded also to the cicadellids and the aphids, considered as groups.

The inhabitants of the forest above shrub level were not studied. We know from instrumental data that above this stratum, and especially beyond the tops of the low deciduous trees, the summer months show higher temperature, less moisture and greater fluctuation in both factors. If the inherent difficulties of a biotic study of this region could be overcome, the investigation would be very valuable, as it would give us the forms living in the evergreen foliage instead of the population of the deciduous substratum.

The animal population, as far as studied, shows a distinct division into stratal societies. This distribution seems to be determined by a combination of two factors; (1) physical differences between the strata; (2) biotic differences. For example, the alder-spittle insect was dominant in the shrub stratum, where belonged its food plant, a biotic factor; but a change in a physical factor, temperature, caused a downward, stratum to stratum migration. Other instances might be cited. It is probable that the physical factors become of greater importance at critical seasons, such as the later fall. Weese (1924) gives evidence that the lowering temperature and temperature fluctuations serve as a stimulus causing forest-border beetles to migrate first into the interior of the forest, and then downward to the lower strata for hibernation. A downward migration of the young of many herb- and shrub-dwelling spiders is a well-known phenomenon of the later summer (Emerton). On the other hand, a very large number of phytophaga indicate by their vertical distribution that the stratum in which they are found is determined by the presence of the host-plant.

A study of the population shows that many of the species are forest-margin or deciduous underwood forms, rather than animals necessarily belonging to the coniferous forest habitat. Certain other species illustrate the invasion of grassland forms, not found in such forests when remote from agriculture.

The seasonal societies, because of the short and non-critical period when the collections were possible, are less marked than the stratal societies. For the greater number of species, however, and especially for the

predominants, the evidence indicates an early summer (Aestival) maximum, the peak of which had passed at the time the collections were begun, or a late summer (Serotinal) maximum, developing during the latter period of study.

#### SUMMARY AND CONCLUSIONS

The coniferous forest habitat studied shows a very regular stratification of the physical factors of environment; this is most conclusively proven for evaporation, but is in general true for all physical factors.

The evaporating power of air increases with elevation above the forest floor. Based on this factor, the habitat could be divided into three main strata, and each of these into two or more sub-strata..

Temperature increases and humidity decreases in the upper strata, while both show greater range. These results, however, are less conclusive than those bearing on evaporation, and show less stratal difference.

Light intensity increases markedly upward from the forest floor. Its gain in successive layers of deciduous undergrowth is almost comparable to the rise in evaporation.

Biotic response to these conditions is expressed by the composition and distribution of the animal stratal societies. This response, however, is complicated in the various strata by the presence of influences which are themselves biotic. The ultimate response of the animal, at least during summer, is evoked by the combination of physical and biotic factors.

Physical factors are responsible for stratification in proportion to their intensity. During summer conditions in temperate climates, biotic factors tend to attain greater importance. During critical periods of climatic and physical stress, the situation is reversed. Thus under montane conditions, as seen in the Ktaadn studies, physical factors may be dominant at all seasons.

A seasonal series of societies as well as a stratal one, was shown by the animals of the area studied. Numerically the animal population, as a whole, displayed two high points—one in late spring, and another in late summer. These two maxima were not due to the appearance of a second apex for species reaching a high point in the vernal society. Among insects generally, they were caused by the appearance of different species; among spiders generally, by two distinct phases in the life history.

## THE ANIMAL ECOLOGY OF DECIDUOUS FOREST IN WINTER

### SCOPE OF WORK

This portion of the study was undertaken in an attempt to secure data on the animal population of deciduous forest in winter, with special reference to its stratal distribution. It was carried on in the same locality and by the same methods, as the study of Weese (1924), made in part during the winter of 1921-1922. It should give us an idea of the differences existing between the animal communities of a locality during the same season in different years, when examined by the methods of sampling. Since this study was made in winter, the predominants varied greatly from those based on a complete annual cycle, and the animals present in the largest numbers were the permanent inhabitants of the forest-floor strata; second in importance are the hibernating animals whose stratum of summer activity is higher in the forest, or outside the forest altogether. It should be understood that the data presented is distinctly that of a winter study. It does not give seasonal societies, although it indicates the passing of the last of the autumnal society into the hibernal one; its principal emphasis falls on the response of the animals of the winter society to changes in climatic conditions.

The study was continued to include the prevernal society; the results of this portion of the work will be presented at a later time. Certain groups of animals have not been included in the present report because of the impossibility of getting determinations on them in time; these include the Cicadellidae and some larvae.

The generally neglected dynamics of the hibernal society is dealt with in detail because of the following facts: 1, Winter survivors are the basis of increments to the population during the warmer months which follow; 2, winter conditions have important relations to—*a*, survival and *b*, rate of development in spring. The neglect of the study of this phase of insect activity in particular, is responsible for much confusion in economic entomology, and the same may be true for other groups of animals.

In addition to the quantitative study of the invertebrates an attempt was made to take a census of the winter birds and some general observations were made of the mammal population; no reptiles or amphibians were observed during the study.



## ENVIRONMENT

This has been thoroughly described by Weese (1924) and its plant communities by McDougall (1922); these papers should be consulted. The local area embraced in the instrumental study and from which the collecting was done was practically identical with that of the first author. Collecting was commenced before the leaf-fall from shrub and herb strata; most of the ground was carpeted with a rather thin layer of organic debris. By November 6 many of the leaves had fallen from these strata, and a thick layer carpeted the ground. Not until December 22 was the leaf stratum frozen and the soil stratum partly so. On December 29 both were well frozen and covered with a 2 cm of snow, which had increased in thickness to 15 cm by January 5, and to 17 cm by the week following. By January 26 the snow had decreased in thickness to about 12.5 cm, and it remained thus for the next week. A sudden thaw on February 9 left the leaf and soil strata bare and very wet. This condition lasted through the next three weeks, but on March 2, the day of the last collection, leaf and soil strata were again frozen and covered with 5 cm of snow. The general appearance of the habitat during the greater part of the period of study is shown in Fig. 5.

The winter period is of course the time when all animals of terrestrial communities in temperate regions show inactivity as a response, at least in part, to the stressful climatic conditions. Under montane conditions this inactivity is probably absolute, as far as the invertebrates are concerned, and lasts during the long period when the ground is covered with snow and the shallow soil is frozen to the underlying rock. Under the less severe conditions found in northern coniferous forest, the snowfall is none the less heavy and long and the autumn freezing deep; the result is probably a practically quiescent condition of the animal population of the ground strata, perhaps as marked as that of montane tundra and forest. In the more temperate conditions where deciduous forest is the vegetation climax, the winters are less severe and the animal population of the forest floor shows a week to week fluctuation with the changing climatic conditions (Weese). In order to measure these climatic changes, for comparison with the accompanying biotic fluctuations mentioned above, a number of recording instruments were employed, their exposure being similar to that of Weese's instruments.

Temperatures were recorded at three levels. A thermograph was placed in a standard instrument shelter about 0.6 m above the ground in practically the same spot where Weese's 0.6 m instrument was exposed. This also sheltered the clock and recording apparatus of a distance thermograph, whose sensitive bulb was buried under 5 cm of dead leaves and 10 cm of top-soil. Another thermograph was exposed at a height of 11 m in a maple tree nearby. A standard Weather Bureau type maximum

and minimum thermometer was also placed in the instrument shelter; by this all the other instruments were set and checked. The changing of charts and treatment of the data gained therefrom was precisely like that employed in the coniferous forest study, save that the soil thermograph charts were graduated in degrees Centigrade, and therefore did not need the conversion which was employed on the other two. The tree instrument was started the week ending November 17, and its record contains one break, that occurring during the week of January 12. The other two instruments were started the week following. All three records, for the purposes of this report close with the week ending March 9. The results of the study appear in Figs. 21 and 22.

If we consider the air temperature 0.6 m above the ground we see that, starting on November 24, there was a sharp decline the following week, followed by a considerable rise. The next two weeks showed very slight depression but the week of December 29 brought the sharpest change and lowest temperature of the study, the mean temperature falling to  $-14.2^{\circ}\text{C}$ . From this date until February 9 the general trend is upward sometimes by sharp changes; then occurs another depression, followed on February 23 by a rise to the highest point attained by this instrument since the beginning of the study; thence the temperatures fell off gradually until the end.

The record of the instrument in the tree accompanies irregularly that of the lower station, crossing from side to side, but, with a few exceptions, lower with falling temperatures and higher with rising ones. In other words, the temperature at the higher level makes more response to climatic changes, is more extreme. A reversal of temperatures takes place the week of December 8 with falling thermometer, and a second the week of March 2. Reversals on rising temperatures occurred during the weeks of January 5 and March 9.

The records of soil temperatures were not begun until after the fall overturn, or reversal of temperatures between earth and atmosphere; at this time it was already higher than the temperature of the air. With the exception of a slight rise for the week of December 15, the trend was steadily downward until January 12, the earlier fall being sharper than the later ones. The maximum depression of air temperatures for December 29 affected the soil not at all. The trend from January 12 until the end of the study was upward, gradually at first but later more markedly. The final week of the record shows another slight depression, following marked depressions of atmospheric temperature for the week preceding. With the exceptions of the two warm weeks of February 9 and 23, the soil temperature was above the air temperature throughout the period of the study. It was little affected by atmospheric temperature extremes in either direction.

If we now consider the temperature ranges at the different strata, we see that they show more plainly what was indicated in a general way the actual temperatures, that is, that the extent of range increases from the ground upward. From the soil to the atmosphere this is of course very marked; the curve of temperature range for soil never even approaches that of the air strata. The relations between the temperature ranges in the two air strata are less clear, and the curves show more crossing; but the upper stratum, 11 m above the ground, showed on the whole a greater range than the lower, 0.6 m above the ground, and this was decidedly marked for the weeks of highest temperatures. (Fig. 22).

If we compare this data with that taken by Weese in the same stations in 1921-1922, we see a similar type of curve for the same period of the year, consisting of a depression to a minimum point, followed by a general upward movement. The early winter fall of temperatures was somewhat less regular, and the low point was not reached until the early part of February. The minimum was not so low, and the subsequent rise was not so sharp as in 1924-1925. The winter of 1921-1922 was certainly the warmer and somewhat the more uniform of the two.

The relative humidity of the air during winter is probably of much less importance than the temperature, since the latter was so low as to cause freezing of the ground strata during most of the period of study. Even when the ground remained unfrozen the air temperatures were so low that most of the animal population remained, as will be seen, in the ground. Since, however, any factor must be known before it can be ignored, the relative humidity was taken throughout the period of study. The hygrograph used in its measurement was placed in the instrument shelter 0.6 m above the surface of the ground. The sheets were changed, and the computations made as in the coniferous forest study. The data obtained is given in graphic form in Fig. 23. It will be seen that the curve of mean relative humidity does not show any very striking points for the period of study. Its lowest points fall in the dry portion of the late autumn, while the region of its highest general average falls during the periods of rain and thaw in February. The curve of daily variation is high and irregular during the early part of the study but falls rapidly during the winter, and shows less variation from week to week. With rising temperatures the range of atmospheric humidity also increased, but its weekly variations did not, at the end of the time covered by this report, again attain those of the late fall. It seems unlikely that humidity differences of the order shown, when accompanied by such low temperatures as existed, could be of much importance in determining the winter distribution and fluctuation of the animal population in the leaf and soil strata of the ground.

From this it will appear that the changes in the population of hibernating animals in the forest-floor are more probably influenced by the changing temperatures than by any other physical factor. The nature of the population, its stratal and weekly distribution and its predominant species will be considered next.

#### THE BIOTA

The population sampling was done in the same way as in the coniferous forest study, save that during the period when the ground was frozen the upper 10 cm of soil of a quadrat, which alone were examined, were removed entire and examined for the animal population after thawing, instead of being gone over in the field. There is nothing in the data to indicate that the use of two methods in examining this stratum has caused any discrepancies in its record. The results of the quantitative part of the study, as a whole and by strata, are shown as graphs and in tabular form (Table XX). Fig. 24 shows the entire population curve, the separate curves of shrub and herb populations. Fig. 25 gives separately the curves of the leaf and soil animal populations. The weekly collection and analysis of stratal "samples" of animal population was begun several weeks earlier than the instrumental observations.

Beginning with the week of October 9 we have a series of weekly fluctuations, some of very considerable magnitude, lasting until the early part of December. The general mean of these shows, however, a somewhat downward trend, despite the rather high points reached on alternate weeks during late November and early December. The first high point reached was that of October 13. Thence there was a sharp drop to October 27. From this time on until instrumental readings were begun the fluctuations seemed to be determined largely by the air temperature, but to some extent were correlated for the lower strata with amount of moisture in the leaves and soil. For example, the collection of October 6 was taken on a cool day; October 13 was warm and sunny; November 10 showed an air temperature of 13°C. when the field work was done, while the following week, when the smallest collection to date was obtained, the temperature had fallen to 1°C, and there were flurries of snow. Beginning with November 24, the population curve falls with falling temperature during the next week, and rises with rising temperature the week following. The sharp drop in animal population during the weeks of December 8-22 was apparently caused in part by gradually falling temperatures in the soil and in part by the dry condition of the leaf and soil strata; the great drop in air temperature did not come until a week later. Beginning with December 22, the total population trend is upward, though many fluctuations, until almost the end of the study. The population apices roughly coincide with temperature apices, especially where these

last were unusually high. At the very close of the period of study the population fell sharply to the very minimum observed; this accompanied a temperature fall, moderate in amount but very sudden, from one of the highest points observed during the whole study.

The population as a whole appeared to fluctuate in numbers with climatic changes, especially temperature. Air temperatures seemed to be of more importance during the early part of the study, when more of the population was in the shrub and herb strata. Later changes of atmospheric temperature were less directly active on the animals, now almost exclusively confined to the forest floor: Exceptions appeared where sudden and extreme fluctuations of temperature, such as that of February 9, were sufficient to affect directly the temperatures of the forest-floor strata; this seemed more likely to occur on rising temperatures. It might be recalled that the sensitive element of the soil thermometer was buried at the lower limit of the lowest stratum sampled. The leaf stratum was more nearly exposed to the air, and more responsive, we must suppose, to changes in air temperature. There is biotic evidence, as will be seen, that this is so.

The shrub society as might be expected, was of importance only in the earlier part of the study. It contributed especially to the population apex of October 13, less to the lower apex of November 10. Thence the data for this stratum are based on a few hardy individuals and species which ventured out of hibernation during an unusually warm period.

The herb society curve roughly accompanied that of the shrub; differences between the two are probably fortuitous and due to the chance selections of comparatively well or poorly populated areas for sweeping on the various dates. After October 27 this stratum makes no important contribution to the whole population, and its occurrence at all in the record is determined by the same conditions given for the shrub animals.

A glance at the leaf society (Fig. 25) shows at once that after November 10 the population of this layer became the determining factor in the whole number of animals in a sample. Its curve follows closely and falls little short of coinciding with, the general population curve. Its predominants are the predominants of the winter population, and with very few exceptions were the only animals found in any numbers during the study. This is natural when we consider that of the two strata which are of importance in a winter study, this is the one most directly affected by climatic changes, especially in the matter of receiving warmth with rising temperatures. The curve for this society shows two groups of peaks preceded, separated and followed by low points. The earlier low portion of the curve, during the month of October, is probably due to the dry condition of this layer and the retreat of its population deeper into the soil. Indeed, the high value of the soil collections on some of these dates,

the highest found for the soil stratum throughout the study, is strongly suggestive of such a downward migration. With the fall rains and before the coming of extremely low temperatures, the curve for this stratum mounted higher and with minor fluctuations due probably to temperature, remained high until December 8. It then took part in and largely determined the great descent of population during the two following weeks, which has been already discussed. In fact, from this point on its story would be that of the population as a whole, of which it made by far the greater part.

The soil population was the most uniform of the animal societies. Its early high points have already been discussed. Its high points during the winter, none of which are so marked as to be entirely above suspicion as caused by the selection of unusually good quadrats for collecting, do nevertheless show apices which generally coincide with the apices for the leaf stratum. The most important exception to this is the collection of February 9, where the lowest soil pupulation of the study occurred coincidentally with the highest leaf population. This was one of the most marked temperature fluctuations observed, and perhaps called into activity in the leaf stratum a larger proportion than usual of the animals usually remaining in the soil. There is nothing to indicate that the upper 10 cm of soil examined serves during colder weather as a retreat for animals otherwise found in the leaf stratum on the surface. If this were the case, the soil curve would rise as the leaf curve falls. There is no evidence of this. Obviously the animal population of the leaf stratum, on the approach of freezing temperatures, migrates downward to a point below the 10 cm level and probably below the frost line, which was not deep at any time.

At the same time it should be noted that the animals found hibernating in the forest-floor showed, practically without exception, a complete absence, as far as could be observed, of harmful effects of low temperatures. Throughout the greater period of the study the leaf layer was frozen, and the upper portion of the soil more or less so, and frequently frozen as hard as ice. Animals of all sorts, mollusks, myriapods, arachnids and insects, when thawed out of the leaves or the solid masses of frozen soil moved about actively and seemingly with vitality unimpaired. There was nothing in their appearance or behavior to indicate any marked winter mortality. Under these conditions of cold and freezing neither decomposition nor destruction by scavengers could take place, and it seems safe to infer that the scarcity of intact dead animals, coupled with the uniform activity of the live animals when thawed out of the frozen matrix, indicates that the death-rate among hibernating invertebrates frozen in the forest-floor is not as high as has been supposed. Of course many animals habitually pass the winter below the frost-line; such ani-

mals would be presumably destroyed or at least debilitated by exposure to freezing temperatures. The above remarks apply, however, to the animals normally found hibernating in the forest above the freezing level, and the observations on which they were based were made in what was an unusually severe winter for the locality.

To summarize the winter activities of the animal societies we might give a general account of what happened during the present study. At the time when collecting was commenced, the total population had fallen much below the autumn maximum caused by the influx of forest-border species coming in to hibernate in the shelter of the forest (Weese). There remained still, however, some evidence of this in the case of individual species. The animals left on the shrubs and herbs were few, and rapidly became fewer, crawling for shelter into the leaves and soil. The resident population of the soil and leaves, moisture-requiring and dark-choosing (Shelford, 1913) invertebrates, were few in number to the depths collected, but appeared more numerous than usual in the soil and correspondingly less so in the leaves. With the increase of available moisture in these lower strata, and before the ground was much affected by the chilling of the air, the population of invertebrates, largely residents in the leaf layer, rose, and with minor fluctuations remained high for a period of weeks. It then rather abruptly decreased with the chilling and possible with the drying of the leaf layer. The minimum point of population preceded the minimum point of air temperature by a week. From this time on the population, now consisting almost wholly of the leaf stratum animals, rose gradually, though fluctuating from week to week, until February 9, when a warm rain cleared away the snow and thawed the frozen soil and leaves. The population mounted at the same time to the largest total observed in the study. A lower temperature followed the next week, and the number of animals fell to less than half, presumably mostly re-treating into the earth deeper than the samples were taken, though there is evidence that a few remained in the surface soil. A second high point the following week accompanied another rise in temperature; this was still caused by numbers of animals appearing in the leaf stratum. With the sharp fall of temperatures the week following the leaf and total populations dropped almost to *nil*, most of the animals reëntering the deeper layers of the soil, but a few remaining in the upper 10 cm. Throughout the period the soil population had undergone the least fluctuations. The warmest days had brought up a few animals to the herb and shrub strata; these disappeared with the falling temperatures.

The animals named as predominants below must be considered as entitled to that term only with reservations; that is, they are *numerical* predominants, the most numerous animals found in the area at the time

the study was made. Second, they are *seasonal* predominants in part; some of the species listed would not be found in the deciduous forest floor save at the season of hibernation. The most numerous species, however, are permanent residents of the lower strata of this habitat. With these reservations in mind and with the repetition of the statement that most animal predominants do not "control the habitat" as some plant predominants do, we may consider the species listed as good and valid seasonal and stratal animal predominants. Some of them are more than this.

The following species are listed by their stratal occurrence and the invertebrates are given in their respective societies in order of their relative abundance; the seasonal and in some cases the stratal distribution is plotted for most of the species in the plates.

#### Subinfluents:

Tomocerus (Leaf) Society: Enchytraeidae (undetermined), *Tomocerus flavescens* Tullberg var. *americanus* Schott, *Onychiurus subtennis* Folsom, *Carychium exiguum* (Say), *Malthodes* sp. (larva), *Telephanus velox* Hald., *Lygus pratensis oblineatus* (Say), *Isotoma* sp., *Vitrea indentata* (Say), *Anyphea rubra* Emer. (juvenile), *Cleidogona caesiaannulata* (Wood) (juvenile), *Leptothorax curvispinosus* Mayr., *Zonitoides minuscula* (Binney), *Gastrocopta tappaniana* (C. B. Adams), *Dictyna volupis* Keyserling, *Nitidula rufipes* (L.), Phalacridae (undetermined), *Zonitoides arborea* (Say), *Carychium exile* H. C. Lea, *Nabis fesus* (L.), *Leptocera* sp., *Linotaenia chionophila* (Wood), *Scytonotus granulatus* (Say), *Tipula* sp. (larva), *Phyllotreta sinuata* (Steph.), *Meracantha contracta* (Beauv.) (larva), *Myodochus serripes* Oliv., *Cantharis* sp. (larva), *Fannia* sp. (juvenile); *Peromyscus leucopus novaboracensis* (Fischer), *Blarina brevicauda* (Say), *Sylvilagus floridanus mearnsii* (Allen).

Fontaria (Top-soil) Society: *Lasius flavus* Fabr. subsp. *nearcticus* Wheeler, *Fontaria virginensis* Dry., *Pokabius bilabiatulus* (Wood), *Onychiurus armatus* Tullberg, *Onychiurus fimetarius* (L.), *Ptilodactyla serri-collis* (Say); *Scalopus aquaticus machrinus* (Rafinesque).

A few species are listed which appeared at the beginning of the collections in the

Linyphia (Herb) Society: *Linyphia phrygiana* C. Koch, Lathrididae (undetermined), *Tetragnatha* sp., *Epitrix brevis* Sz.

A single mammal was noted as characteristic of the winter.

Sciurus (Tree) Society: *Sciurus niger rufiventer* (Geoffroy). The above lists include only a small proportion of the species taken in the weekly collections; they do, of course, include all species taken in such numbers as to entitle them to status as predominants in the societies where they occur.



### Predominants of the Tomocerus (Leaf) Society

#### Enchytraeidae (Fig. 30, Bc and d.

This family of worms, on which it was not possible to secure determinations, was decidedly a predominant group in the leaf society, where they appear to be characteristic animals (Welch, 1914). They are constant residents, but may withdraw into the soil if conditions become unfavorable. They were found in the leaf layer during the early collecting, but seemed to retreat into the earth when the ground became drier during the fall, becoming very scarce in the collections until the late rains. They then became numerous in the leaves and fairly so in the soil, their numbers contributing much to the high populations of November 24 and December 8. With falling temperatures they became few in the leaves, some apparently lingering in the top soil, and finally disappeared from the collections altogether. They appeared again during the warm and wet week of February 9 and make up a notable part of the high curve for that date, disappearing almost completely with the low temperature and general population decline of the following week. They again became abundant the week following, and disappeared entirely during the cold Monday when the last collection was taken. From the numbers of the animals that may be found in the dead leaf layer during warm and wet weather, it may be that we have here not only a numerical but also a real stratal dominant, the gross effects of whose activities on the gradually decaying layer of organic debris may be considerable.

*Tomocerus flavescens* Tullberg var. *americanus* Schott. Fig. 30, Ab, c and d.

The seasonal and stratal distribution of this spring-tail is very suggestive of that of the Enchytraeids. In fact, its close agreement with those animals in its response suggests an analogy to the "behavior agreement" found by Shelford for aquatic and terrestrial animals (1913, 1914). The animal seems to be somewhat more tolerant of unfavorable conditions, however, remaining in the leaves and top soil in considerable numbers during periods of freezing, from which it emerges into activity, at least, unimpaired. It was rarely taken on the herbs. It seems likely that in this species, as well as in the other numerous Collembola, we may have real stratal predominants. Their numbers, constant presence and food habits suggest that the part they play in the organic changes going on in the forest-floor may be by no means as small as their size and lack of "economic importance" in the usual sense might lead one to suppose.

*Onychiurus subtenuis* Folsom (Fig. 29, bottom curve).

This species appeared for the first time with the rising temperature of January 5. Thence it fluctuated in small numbers until February 9, when it took an important part in the maximum of that date. Along with other species, it fell off sharply the following week, but, unlike most

others, it disappeared completely the warm week following, when most other species took more or less part in the second population rise. It might appear that we have here a less hardy species than *Tomocerus flavescens* which, called out of deeper hibernation by the unusually warm weather, was chilled back during the following cold snap, from which it was unable to recover.

*Carychium exiguum* (Say) (Fig. 26, I).

This snail was present in the largest numbers of any mollusk, but neither it nor any of the remaining forms was in the same order of abundance as those just named. It was present in the leaf layer in moderate and fluctuating numbers from the time of the autumn rains and consequent moistening of this layer until the end of the study. Its single high point coincides with the second population apex of February; it increased only slightly at the time of the first and greatest February rise. Inasmuch as these were periods of both increased soil moisture and rising temperature it would be difficult to assign to either the rise, which was general for several species of mollusks; but the general habits and responses of the animals leads one to suspect the former.

*Malthodes* sp. (larva) (Fig. 28, E)

This cantharid larva was the most abundant beetle; it appeared early in the collections and with increasing frequency and in increasing numbers as the study progressed. Its first marked increase came with the slight but distinct population rise that followed the low week of December 22. Its second maximum, curiously enough, falls on the week of moderately low temperatures that intervened between the two high weeks in February.

*Telephanus velox* Hald. (Fig. 28, Db, c, and d.)

This species is of particular interest as studied in detail by Weese in 1921-1922. He found it on the herb stratum October 3, and in the leaf stratum throughout the winter, with a maximum on November 7. Save that the hibernation migration took place later, the findings for the beetle in 1924-1925 were remarkably similar. It was swept from the herbage October 13, and showed an extraordinary maximum in the leaf stratum on November 24. Thence it appears in varying numbers all winter, its only other marked increase coinciding with the first "high" in February. This species was also taken in the ground from time to time and its appearance there in some numbers preceded the February rise.

*Lygus pratensis oblineatus* (Say) (Fig. 27 Fa, b, c and d.)

The tarnished plant bug appeared in considerable but varying numbers throughout the study, but for the winter season is undoubtedly to be classed in the leaf society. It appeared in increasing numbers on the shrub and herb strata during the early part of the study, disappeared from these strata in the order named and became abundant in the leaf stratum,

where its numbers underwent considerable fluctuations from week to week. Its first and greatest increase there coincided with the general rise following the period of lowest populations. Thence its numbers fell off sharply and then with rising temperatures gradually increased until February 16, its high points not exactly coinciding with the highest temperature points. On the date when the highest temperatures occurred, however, a few individuals appeared in the herb and even ascended to the bare shrubs. A few individuals also appeared in the soil early in the season. The fall distribution of this insect among the strata indicated an inward migration from the forest border, followed by a downward migration into the leaves, similar to that described by Weese for several species of forest-border beetles in this same habitat.

*Isotoma* sp. (Fig. 29, Cc and d.)

This spring-tail appeared in small numbers in the soil about December 29, and a few were taken in the leaves February 2. The great rise took place on February 23, and took part in the general high curve for that warm period. Its numbers at once declined, and it was not taken again in the collections.

*Vitrea indentata* (Say) (Fig. 26 Hc and d.)

This snail was found throughout the winter in hibernation in the leaf layer; its fluctuations during the early part of the season are probably not significant. At the time of the coldest week, the animal disappeared from the leaf stratum but was taken in some numbers from the soil. The maximum for the winter fell on the "high" of February 23, and was probably determined chiefly by moisture.

*Anyphaena rubra* Emer. (juvenile) (Fig. 26, Ca, b, c.)

These young clubionids hibernate habitually in the leaf stratum, where they were taken in varying numbers throughout the winter. Their records of stratal occurrence show a downward migration from shrub and herb strata to the leaves, during the whole autumn period. A few specimens were taken from the herb level on warmer days during the winter.

*Cleiogogona caesioannulata* (Wood) (juvenile). (Fig. 31 Cc, d)

This diplopod is a characteristic species of the animal society inhabiting the humus and ground litter on the deciduous forest floor (Adams, 1915; Weese, 1924), where it exercises subinfluence in altering the compounds produced by plant decay (Adams, loc. cit., and reference to Cook (1911c). It appeared in the samples taken by Weese during July and again in early November. In the writer's collections, *Cleiogogona* appeared first in the soil stratum on November 17, in the leaf stratum the week following (when it was not taken in the soil), and it increased in numbers in the leaves through the week following, reaching the high point for the collections on December 8. The following week the species disappeared entirely from the leaf stratum but were still present in considerable numbers

in the soil. They then disappeared entirely from the collections until the warm week of February 9, and for the next two weeks they were taken in some numbers in the leaves. The cold week of March second yielded none of these animals in the leaf stratum, but a considerable number remained in the upper 10 cm of soil. They were not taken again during the study. This species, as far as its stratal distribution is concerned, seems to behave like some of the mollusks. It was absent from the upper strata during the dry weather of the fall both in 1921 (Weese) and 1924. It reached its maximum when the forest floor was moist from the late autumn rains, and disappeared during the coldest part of the winter. Early spring rains and warm weather brought up numbers of these animals into the forest floor litter, but with falling temperatures they passed into the soil and thence into deeper hibernation at levels where they were not reached by the methods of collecting.

*Leptothorax curvispinosus* Mayr.

This ant is an example of a resident stratal predominant; maxima represent colonies of hibernating individuals which chanced to be in the quadrats selected for study on the dates in question. They are included because they represent a fairly numerous and characteristic species and suggest the discontinuous distribution of animals with such mores over the forest floor.

*Zonitoides minuscula* (Binney) (Fig. 26, G)

This land snail was collected in fluctuating numbers from the leaf stratum during the entire winter, not appearing until after the fall rains. The first rise in numbers was that of December 8, and was a part of a general population high, accompanied by a considerable rise in mean temperature; the second high point coincided with that of *Vitrea indentata* and was no doubt due to the same factor.

*Gastrocopta tappaniana* (C. B. Adams) (Fig. 26, F)

This species showed a rather different type of distribution from that of the species just described. It showed a high point early in the season, probably correlated with the moisture incident on the autumn rainfall, and then disappeared entirely from the collections until the "highs" of February, when it was again sparingly taken.

*Dictyna volupis* Keyserling (Fig. 26, B-a-b, and c.)

These young Dictynids showed the same stratal and seasonal distribution as *Anyphaena rubra*, already described, save that they did not appear above the leaves on the warm days in the latter part of the winter; they sometimes do so, however (Weese, 1924).

*Nitidula rufipes* (L.) (Fig. 28, C).

This species was found hibernating in varying numbers in the leaf stratum throughout the winter; it responded to the conditions existing

on February 9 and 23 by appreciable increases in numbers, no doubt called forth from deeper hibernation.

*Phalacridae* (undetermined)

The numbers and seasonal and stratal distribution of these beetles indicated the same inward and downward migration described by Weese for *Phalacrus politus* in this habitat; they appeared first on the shrubs, later on the herbs and thereafter and throughout the winter in hibernation in the leaf stratum. In the absence of specific determinations, their occurrence has not been further studied.

*Zonitoides arborea* (Say) (Fig. 26, E)

This species was taken only towards the latter part of the study and its only marked increase in numbers fell on February 23, the period when most of the mollusks showed a high point.

*Carychium exile* H. C. Lea (Fig. 26, D)

The appearance of this snail in the collections agrees well with that of *Gastrocopta tappaniana* but with no other species of mollusk found in any numbers. Its maximum fell in the late autumn, and was probably determined by moisture, but it did not appear again in the collections. It was found exclusively in the leaves.

*Nabis ferus* (L.) (Fig. 27 E-a, b, c and d).

Save that it was present in smaller numbers, this common nabid showed the same distribution in the collections as the tarnished plant bug; it appeared in the fall on herbs and shrubs, passed into the leaf stratum, and there remained throughout the winter, a few specimens being also taken from the soil from time to time. Like the plant bug and many other animals it appeared in small numbers above the leaves during warm periods in the latter part of February.

*Leptocera* sp. (Fig. 31, F-a, b, c, d).

This borborid appeared first in the collections at shrub level on October 6, and other individuals of the same species were taken in the herb society for this date. By the next week it had disappeared from the shrubs, but was present in increased numbers among the plants of the herb stratum. Here it appeared for the last time on November 10. It was collected in numbers from the leaf stratum on November 24, but disappeared with the falling temperatures of the week following. The temperature rise of December 8 was accompanied by considerable numbers of these flies in the leaf society. The following week they had disappeared from the leaves but a few were found in the soil. They were not taken thereafter. The data suggest a downward migration similar to that observed for other species, accelerated by falling temperatures and arrested by rising ones, to the level of hibernation. Weese took *Leptocera evanescens* Tuck. from ground and herb strata at various times through the winter of 1921-1922.

*Linotaenia chionophila* (Wood) (Fig. 31, A-c, d).

This centipede was a common animal of the leaf society during the fall. It appeared first in the soil collections, perhaps because of the dryness of this stratum during the early part of the study. Thence on it was common in the leaf stratum until the temperature drop of December 1, when it disappeared from the collections for the next two weeks. On December 15, when the temperature of the soil had risen somewhat, a few appeared in the soil stratum, and a few more were collected in the leaves during the warm week of February 9. Weese found this species on the forest floor from time to time during the winter.

*Scytonotus granulatus* (Say) (Fig. 31, E-c, d).

This millipede was a characteristic animal of the leaf stratum, from which it was collected in varying numbers from time to time during the period of study. Its periods of abundance appear to coincide with even or slightly rising ground temperatures. Specimens were collected from the soil stratum during the latter part of November, but except for this was a leaf-stratum form. Its habitat relations are no doubt similar to those of the other diplopods discussed.

*Tipula* sp. (larva) (Fig. 27, Dc, d)

Crane-fly larvae of the genus *Tipula* were fairly common in the leaves and soil during the fall and late winter. They reached their maximum numbers in the "high" of February 23; there is some evidence that they migrated a short distance into the upper soil during the following cold week and again returned to the surface leaves the next week, which was warm. With the return of extreme temperatures at the end of the study they disappeared, no doubt going to the deeper layers of the soil where they had passed the extreme part of the winter, and where they were not reached by the methods of collecting employed.

*Phyllotreta sinuata* (Steph.) (Fig. 27, C)

Leaf-beetles of the species named were taken in varying numbers and only in the leaf stratus during most of the study; they disappeared, however, for a short period during the coldest weeks.

*Meracantha contracta* (Beauv.) (larva) (Fig. 27, B)

The larvae of this tenebrionid appeared, chiefly in the leaves but a few in the soil, throughout most of the winter. They were more abundant in the early fall, when the ground strata were drier, disappeared about the time of the autumn rains, but were present throughout the coldest weather. They did not take part in the population rise during the month of February. This is a very characteristic influent of the leaf society, often appearing as a dominule in the microhabitats furnished by decaying down timber (Adams, 1915).

*Myodochus serripes* Oliv.

The slender-necked bug appeared on the herbs in the fall, migrating into the leaves and thence into the soil. While most of the specimens were taken in the leaf layer, this was in the fall and there is reason to suppose that most of these animals hibernate deeper. The species was taken from among the dead leaves of this habitat by Adams during the season of hibernation (Adams); as he remarks, and as is true for certain other species found here by the writer and by Weese (1924), such examples "show how during the hibernating season many animals are to be expected here which at other seasons live in other habitats."

*Cantharis* sp. (larva) (Fig. 27, A)

The larvae of this cantharid beetle were taken almost entirely from the leaf stratum at intervals during the whole series of collections. They showed their maximum increase of population during the week of February 23, when so many species appeared in increased numbers.

*Fannia* sp. (juvenile) (Fig. 31, G).

The larvae of *Fannia* were very characteristic inhabitants of the layer of forest floor litter, the only stratum from which they were collected. They gradually decreased in numbers as the soil temperature fell, disappearing entirely from the collections during the coldest period. A few were taken during the middle of February; this was a period when the soil temperature was slowly and steadily rising.

Predominants of the Fontaria (Top-soil) Society

*Lasius flavus* Fabr. subsp. *nearcticus* Wheeler.

Two small communities of this ant were captured entire on October 13 and November 10, respectively. The same general remarks apply to them as to *Leptothorax curvispinosus*.

*Fontaria virginiensis* Dru. (Fig. 31, D-c, d).

This large myriapod is common in the humus and forest-floor litter of deciduous forest (Adams, 1915; Shelford, 1913). During the winter it appeared in the leaf litter only once in small numbers, and a few were taken from this stratum early in the collecting. With these exceptions, the species appeared only in the soil for the period of this study. The largest population appeared at the time of the general population increase during the warm weather of February, and accompanied a gradual rise in soil temperature. Two earlier but lower apices for this species, falling on December 1 and January 5, did not appear to be correlated with any particular changes in physical factors. They were perhaps due to the fortuitous selection of unusually well-populated quadrats. The species was not taken after the cold weather of March, until the close of the period of study on which the present report is based.

*Pokabius bilabiatatus* (Wood) (Fig. 31, B-c, d).

This centipede is reported by Weese for his ground stratum in July, October and late November. The writer found it in the soil stratum during the early part of the study, where it was a constant resident until it disappeared on December 8 with the lowering of the soil temperature. There is evidence of a stratum-to-stratum migration upwards from soil to leaf-litter during the week of November 10-17, followed by a return downward to the soil. The two warm, wet weeks of February 9 and 23 brought numbers of these centipedes up into the leaf-litter. With the colder week of February 16 and the decided temperature drop of March 2, the curves show that the animals dropped entirely out of the leaf society, and were present in smaller numbers in the soil. Doubtless most of them had withdrawn into the deeper soil where they had spent the colder weeks preceding.

*Onychiurus armatus* Tullberg. (Fig. 29, B)

Spring-tails of this species occurred in some numbers in the soil stratum during the latter part of January and the first of February; they were not taken at any other time.

*Onychiurus fimetarius* (L.) (Fig. 29, A).

The maximum abundance of this spring-tail fell on March 2, practically the only time it was taken. This was a very cold day, and the other species of Collembola, some present as numerical predominants during the preceding warm week, had disappeared.

*Ptilodactyla serricollis* (Say) (Fig. 28, B)

This beetle was collected from time to time through the entire period of study; it was sometimes taken from the leaf stratum as well, but was more common in the top-soil.

#### Predominants of the Linyphia (Herb) Society (Autumnal)

*Linyphia phrygiana* C. Koch. (Fig. 26, A)

Young of the hammock-spider were collected from the shrub and herb strata at various times during the fall and early winter, disappearing with increasing cold into retreats where they were not reached by the collecting methods employed. A scanty appearance of the species occurred during the warm week of February 9.

Lathrididae (undetermined)

Lathridid beetles of undetermined species were fairly common on the shrub and later on the herb stratum in the fall and early winter; the last were swept from the herbs on December 8. They were not taken thereafter nor in the lower strata.

*Tetragnatha* sp.

Young *Tetragnathas* were constantly taken from the herb stratum during the early part of the study; they disappeared on December 8,



reappearing in small numbers at herb level on February 23; they were not taken at any level during the intervening period.

*Epitrix brevis* Sz. (Fig. 28, A-a, b, c and d).

The results obtained for this chrysomelid support the conclusions of Weese on its autumnal migration and hibernation. Small numbers were present at shrub and herb levels on October 6, and large numbers on the herbs the week following. They then entirely disappeared from all strata until the warm week of December 8, when a few were taken in the leaf stratum. The species was not again taken above the soil stratum, and rarely there. Evidently hibernation is deep, as Weese suggests.

### Vertebrates of the Winter Society

Vertebrate animals, except birds, are of few varieties and not particularly abundant in individuals in the area studied. The reason for this has been given by Weese; the forest was depleted of much life by a period of heavy grazing and consequent depletion of ground cover, and on the removal of this factor the isolation of the tract prevented the reestablishment of forms which had once become extinct or migrated. The forms which remain, however, are those characteristic of the habitat in an untouched condition.

No attempt was made to study the mammal population in detail; the following notes are from general observations made in various ways of the presence of common species, based on sight records, tracks in snow, partly-eaten food, etc. It will not be possible to do more than give a general idea of what mammals are present in this and similar habitats of the region, and the relative abundance of the more common species. The two most abundant mammals are unquestionably the white-footed mouse (*Peromyscus leucopus noveboracensis* (Fischer)) and the short-tailed shrew (*Blarina brevicauda* (Say)). The writer is indebted to Dr. M. S. Johnson for this information, gained in extensive trapping with both box and guillotine-traps for the former animals, that they are much the more abundant of the two. There is a great gap between the numbers of these animals and those of the next most numerous species, the fox-squirrel (*Sciurus niger rufiventer* (Geoffroy)) and the cottontail rabbit (*Sylvilagus floridanus mearnsii* (Allen)), of which the former is probably somewhat the more abundant. Less common appears to be the mole (*Scalopus aquaticus machrinus* (Rafinesque)), although its work was frequently encountered in digging out the soil collections. These represent the mammals that are definitely known to inhabit the tract under consideration. Other species, characteristic of the habitat (Wood, 1910) and some of them known to exist at present in similar wooded tracts within a few miles, are: the opossum (*Didelphys virginiana* Kerr), the chipmunk (*Tamias striatus lysteri* (Richardson)), flying squirrel (*Sciuropterus volans*

(Linnaeus), red fox (*Vulpes fulva* Demarest)), raccoon (*Procyon lotor* (Linnaeus)), weasel (*Putorius noveboracensis* Emmons) and probably the long-tailed shrew (*Sorex personatus* I. Geoffroy-Saint-Hilaire).

Of these animals the only ones which would be likely to directly affect the rest of the animal community during winter are the short-tailed shrew and the mole. The activities of the latter at this season of the year are confined to levels below those where collecting was done. The shrews, however, probably feed to a very considerable extent on the hibernating population of invertebrates in the forest-floor.

During the period between January 5 and March 2 an attempt was made to take a bird census of the area under study. The area was visited for this purpose at least weekly and frequently oftener. An attempt was made to arrive at a quantitative result as well as a qualitative one; great conservatism was observed in making the estimates, which are therefore believed to be well on the side of safety. The results are given in Tables XXI-XXV, Table XXI gives the estimated numbers for species constantly present, their location in the forest and stratal occurrence. Table XXII gives the same information for frequent visitors, Table XXIII for occasional visitors, and Table XXIV for a few early migrants observed during the latter part of the study. Table XXV gives the list of species with numbers and dates when observed.

These data will be discussed only in relation to the effect of the winter birds on the hibernating invertebrates. Considering the species which are present in any numbers it appears that there are few if any of the actual residents which would be expected, from our knowledge of their food habits, to feed on the large population of insects and other invertebrates in the leaf stratum. The important birds are either seed-eaters or insect-eaters which, like the woodpeckers, get their food from the tree stratum. The flicker may occasionally feed on the forest floor, for it is sometimes seen there, but its doing so is apparently exceptional. It does not seem likely that the birds listed, either from their numbers or their food habits, can produce much effect on even the animals of the leaf stratum, and we know that many species hibernate out of reach entirely.

#### DISCUSSION AND SUMMARY

The present study began before the close of the autumn migration of animals from the forest border and from the herbs and shrubs of the forest itself into the leaf layer for hibernation. This migration had well progressed before the temperatures had become extremely low, but was no doubt incited by their gradual decline during the first part of the period of study. As far as this migration concerns forest border species, those migrate inward on their own strata and then downward to the forest

leaf-layer; this was determined by Weese for a number of beetles and the writer obtained evidence in the same direction for some other species. The downward migration may be delayed on the herb level, in the leaf level or in the upper soil, or the animals may disappear at once from the shrub level into deeper hibernation. As far as the forest-border insects are concerned, the movement towards winter quarters seems to be correlated with temperature changes, to be continued rapidly on falling temperatures and arrested more or less on rising ones.

Other animals, living earlier in the season in the upper strata of the forest itself, migrate downward at the same time. They behave in a very similar way as far as the effects of temperatures are concerned, entering the leaf stratum more promptly with falling temperatures. The evidence indicates that different species react differently to the factors inducing hibernation, and that the reactions for a given species are constant from week to week and from year to year. Certain forms migrate at once to the deeper strata and are not seen again until the time of emergence in the spring. Other species remain comparatively near the surface, in the top-soil or leaf strata or both, and seem to fluctuate in abundance in activity with the changing conditions. Ordinarily these animals are the ones which determine the fluctuations in numbers found in samples.

Extreme changes in either direction may cause marked differences not only in the size but also in the composition of the samples. Extreme cold in the soil layer reduces the population to some extent, but less than might be supposed; temperatures rising to the thawing point, especially if accompanied with abundant moisture, bring up a large population, composed in part of hibernating animals from various strata but mostly consisting of the moisture-requiring permanent residents of the forest-floor. On the other hand, cold or dryness in the forest-floor markedly reduces the numbers of the resident enchytraeids, mollusks and spring-tails. That certain species are much more sensitive than others is indicated by the very different seasonal distribution of various species of *Collembola* and mollusks throughout the period of study.

The changes in temperature, as shown by the curves, are much more gradual in the forest floor than in the air above it. Indeed, it is evident that the decline does not trap any great numbers of animals in the frozen upper layers, and does not seem to affect adversely most of the animals which do remain there during freezing. The invertebrate population of the upper ground strata, once the freezing point is approached, seems to consist of species which are able to tolerate complete freezing with little harm, but before this condition is reached many animals migrate downward. On the other hand, very warm periods call up from deeper

hibernation species never found during winter weather; on the return of the cold, these forms soon disappear, returning to the regions lower in the ground, probably below the frost-line.

The different reactions of various species to changing conditions of the physical environment is of great interest. We must assume that the winter is a period when biotic influences are at their lowest, and the maximum role is played by physical factors. To this extent the changing earth temperatures may be looked on as a series of natural experiments on the effect of changing the physical environment. The animal responses thus evoked appear distinct for various species of the same group. Thus certain species of Collembola, mollusks, etc., present at one period in distinctly predominant numbers, during other periods disappear wholly or in part and are replaced by other species from these same groups. These differences in predominants can hardly be considered societies, in the sense of the use of that term by plant ecologists. They are too brief, and their disappearance is probably caused merely by local withdrawal to deeper areas. They represent the response of some species to a particular complex of physical factors to which other species of the same group are negative or neutral. Such responses may be as definite specific characters as morphological ones.

It is an ecological axiom that animals react most accurately to physical changes of kinds affecting them under natural conditions. The invertebrate population of winter forest is a stratal population occupying, generally speaking, only the leaf and soil strata. We should expect to find its members responsive to changes within those strata, and to a large degree this proves true. Thus the curve of population only roughly coincides with the curve of air temperature, and this largely because the leaf stratum, in contact with the atmosphere, has its temperature more or less directly affected thereby. So far as could be observed there existed no correlation between animal population and atmospheric humidity; the changes in this factor are little indicative, in winter, of conditions in the soil and leaf strata. But soil and leaf moisture, though it was not measured and could not be separated in its effects from temperature, appears to be a factor of importance.

It has been said that biotic influences were at their lowest among the hibernating population of forest floor invertebrates. Most of the animals were in a quiescent or dormant condition when collected, although they soon revived when exposed to warmth. There was no evidence of activity among spiders, nabids or other predatory species, and on even the days when conditions were such that some animals were seen among the dead herbs and leafless shrubs, they were rather torpid. As has been seen, the effects of the activity of vertebrates on the forest floor animals are probably negligible.

## CONCLUSIONS

Temperature is the climatic factor which seems to be of greatest importance to the winter forest population; this factor is well stratified, the higher strata showing greater extremes and lower mean temperatures. The stratum whose temperature is of importance to hibernating animals is the ground; here is the highest and most uniform of the three stratal temperatures studied. Atmospheric temperature is of importance only in so far as it affects the ground, and especially its leaf stratum.

There is no evidence that atmospheric humidity shows any direct correlation with the population of hibernating animals.

Moisture present in the forest floor appears to be a factor in the weekly variations in the numbers of animals in the samples. An increase of moisture in winter, however, is almost always accompanied by a rise in temperature, and the separate effects can only be inferred.

Biotic factors seem to play little or no part in the weekly fluctuation in numbers. Invertebrate predators are themselves quiescent at this time. The vertebrates feeding on the forest floor insects are not present in sufficient numbers in winter to have any marked effect.

The first response of animals to the falling temperatures is the descent of shrub animals to the herb level; this is characteristic both of inwardly migrating forest-border species, such as certain beetles, and of true forest shrub animals, such as many young spiders. From the herb stratum the animals pass downward into the leaves.

Some animals remain in the leaves for the entire winter; others until this layer becomes colder; others make only a brief stop; while the remainder pass directly into the soil beneath. Behavior in this regard appears to be a species characteristic. The members of the last group do not reappear, as a rule, during the winter.

The animal population fluctuates somewhat between the leaf and upper soil strata but less than would be expected. Conditions sufficiently severe to markedly reduce the number of individuals in the leaf usually drive the animals deeper into the earth than the upper 10 cm of soil. The reverse is also true; conditions which cause any noticeable increase in the leaf population do so by affecting the soil deeper than the top layer.

Many resident animals of the forest-floor show very marked response to changing physical factors—especially temperature and moisture—by migrating vertically. Such animals as spring-tails, Mollusks and enchytraeid worms are the numerical dominants of the forest-floor strata in winter, and probably at other times as well. From their huge numbers and constant presence some of these animals may be considered as pre-dominants of these stratal socies.

After the fall migration downward, the herb and shrub socies are insignificant in their contributions to the general population. The soil,

in its upper 10 cm., gives a rather uniform but low animal count. The leaf stratum varies enormously and determines, by its curve, the curve of the total population.

The animals in the leaves and upper 10 cm of earth are uniformly found in a condition of dormancy from cold. They are frequently frozen solidly into the earth and leaves for weeks at a time. There is no evidence from the present study that this exposure to low temperatures is injurious to them, as they become active when thawed out.

The large number of animals often recorded for a single week is partly due to the presence of one or more species which appeared exclusively at that time. This seems to indicate a capacity for response quite different among different species in the same group. It suggests, in addition to the recognized, morphological differentiation, physiological distinctions between species. The data at hand relative to the winter populations, etc., will be compared with that of Weese and others later.

## GENERAL DISCUSSION AND SUMMARY

The process of biotic succession tends constantly to cover bare areas of the earth's surface with a climax biota of vegetation and its animal inhabitants; this climax is determined primarily by climate (Clements, 1920). Animal succession over such areas is correlated with—and to a large extent determined by—plant succession. Under favorable conditions the climax may develop swiftly, its dominants becoming well established in a comparatively few years (McDougall, 1918). Under greater stress of unfavorable climate and soil the subclimax stages may be of very long duration; the montane tundra studied in the first part of this survey is a preclimax stage of coniferous forest showing arrested development (Harvey, 1903).

The vegetation climax in all the areas under consideration is forest; for the first and second studies it was northern coniferous forest (northern mesophytic evergreen of forest of Shreve and Livingston, 1921) and for the second it was deciduous forest (McDougall, 1922). The general succession of biota following the last glacial retreat is pictured by the present day distribution of biotic types from the Arctic Ocean southward; that is to say, tundra, coniferous forest and deciduous forest, in the order named (Adams, 1905). We are therefore justified in considering that a study of these stages should give some idea of the process of animal succession accompanying the slow northward migration of climaxes at the close of glaciation. If we substitute for the subarctic low tundra the alpine high tundra of the northern Appalachians, we still have a comparable series, since a large proportion of the characteristic species is common to both.

Beginning with bare rock areas, which we may assume not to differ essentially as biotic habitats from similar areas left by the retiring ice-sheet, we find thereon a scanty covering of lithophytic plants, independent of animals. The animals present are principally small lichen-feeders and lycosid spiders belonging to species characteristic of this habitat in high and low tundra regions. Climatic conditions are extremely severe, temperatures ranging as much as 28°C. between sun and shade and wind velocities approximating 110 miles per hour. In the absence of any appreciable plant cover, these must exert a maximum effect on animal life. The dominant animals live in openings among and under the rocks, and their habits are adjusted to this type of life; the community thus consists of one stratum only. Succession from this stage waits on the formation of a soil, in which process both biotic and physical factors

are involved. There is evidence that the latter are of particular importance in these early stages, although the former cannot be ignored.

With the formation of finer rock fragments and the retention among them of a coarse granitic soil, to which the pioneer biota contribute a sparse organic component, we have the establishment of the early tundra, a shallow sod overlying rock and hence comparable to arctic low tundra, which overlies continually-frozen soil. On this sod and largely composing it are characteristic plants, among which grasses and sedges are most conspicuous. The whole furnished the home for an animal associates of different species and life histories from those inhabiting the rock area. The plants furnish a more abundant food supply and the dominant animals are species of Cicadellidae which are characteristic of such host-plants. Climatic stress is still as severe as on the rocks, but the soil and alpine grasses furnish a partial shelter during the frequent storms and low temperatures of the short summer, as well as a means of retaining moisture and heat. During the winter the thin cover of earth and dead herbage furnishes a place for hibernation; that it is efficient shelter is indicated by the numerous and varied population which appears in the late spring on the high tundra, as well as by studies made on animals hibernating in the frozen upper layer of earth in other habitats.

This associates has really two societies, soil and herb, but the animal population seems to leave the shallow soil almost *en masse* during the warm period of the year. Thence on, the process of succession is increasingly dependent on the biotic factors; the climatic factors, local or regional, are retarding in their effects. With the increase in depth and organic matter in the soil, the latter amounting to 34.5%, a succession to the last stage of tundra community is attained. The capacity for moisture and heat retention becomes greater as the soil and vegetation cover increase in thickness, and hibernation probably takes place under somewhat more favorable conditions. Further succession on the plant side is characterized by the heaths. The animal community is different from that of the early tundra, the differences, however, being chiefly caused by the appearance of phytophaga, especially cicadellids and aphids, associated with the plant dominants, while the grass-eating forms of the early tundra disappear. Although species have changed, there seems no reason to expect a marked change of mores, nor is there any evidence of such a change. The dominant animals are still such as are characterized by short summer activity and long hibernation periods. The heaths are so low as to be of no more than herb proportions, and stratification of the animals remains unchanged. At this stage of succession, in addition to the various associates of invertebrates, some of the vertebrates of the climax forest appear, either as visitors or as more or less permanent residents; especially is this true of small mammals.



With the establishment of the heaths, the tundra series comes to an end. On the increasingly deep soil, due to the deposition of organic material by successive generations of plants and animals, the forest is able to become established, bringing with it forest conditions and forest animals. Here, however, the local climatic factor of wind makes itself felt, and the first forest to gain a footing is the krummholz or elfin-wood. On the advent of its low-growing but dense thickets the habitat changes. Evaporation is reduced, the terrific velocity of air-movement felt in the open becomes much lessened, and temperatures are much more uniform. Perhaps as important as any of these, the new habitat furnishes an abundance of materials for abode. The conditions required for distinct stratification into animal societies become present for the first time, and stratification of the biota is important in all later stages. In the krummholz it is shown especially well by spiders.

The development of the krummholz into climax coniferous forest is not accompanied by any very marked changes in the whole biotic association, although stratification becomes more marked, and there is a large increase in the number of animal species. It is possible that this is due in part to the removal of the conditions of climatic stress which are connected with krummholz formation, but there is no direct evidence that this is so. Rather is it due to the more varied nature of the coniferous forest habitat at lower levels, and its interruption by local habitats, such as bog, meadow, streamside, slash and forest-margin communities. In other words, the animal communities of the climax forest, as compared with those of the krummholz, seem more closely correlated with the massed biotic conditions than any particular physical factors.

Coniferous forest presents a well-stratified habitat, where conditions are much more uniform, for any given period of the year, than those found in any of the preclimax stages. This uniformity is caused in part by the absence of the alpine conditions which have held tundra and krummholz in a subclimax state, and in part by the influence of the forest cover itself. Its most marked physical feature is the constancy and sharpness of the various strata; this is in turn correlated with, and principally caused by, the stratification of plant societies. It is accompanied by a stratification equally sharp, as far as it has been observed, for the animal societies.

Beginning in the forest floor we have in the soil a level of relatively constant temperature, whose summer mean is 14°C, with a mean range of only 2.3°C. Moisture is usually high and light scanty. We must assume that all these factors are present in higher percentage than in the shallow tundra soil. This stratum has a small but rather constant summer population; its winter population has not been studied, but it must be increased by immigrants for hibernation. The predominant

animals are those characterized by a considerable moisture requirement, tolerance of fairly low summer temperatures and a preference for darkness; the ground-dwelling larvae of *Elater* will serve as an example.

Next above this is the leaf stratum, largely composed of dead coniferous needles. Its physical conditions are somewhat different from those of the soil stratum. Temperature averages about 1°C higher than in the upper portion of the soil stratum, but moisture is still abundant; daily evaporation is only .08 cc from the lower part of the leaves. The characteristic animals have a greater capacity for adjustment to changing conditions than the soil animals possess, as evidenced by the fact that they may occur in leaf, soil or, more rarely, on the herbs. A predominant animal in this stratum is the spring-tail *Tomocerus flavescens*. Leaf and soil strata together form a ground society or super-society; physically this is indicated by the fact that the differences between them, while constant, are of moderate amount; biotically it is indicated by the fact that some animals habitually divide their time between these two strata, as temperature and moisture vary.

In the herb stratum there is another and more marked increase in temperature, with a mean temperature of 17.1°C and a mean range of 7°C. Evaporation also rises sharply, reaching 8.2 cc. at herb level. Differences of the same character exist between the herb and shrub and shrub and high bush strata, which have a mean daily evaporation of 11.2 cc and 14 cc respectively; there are smaller differences here, it will be observed, than that existing between leaf and herb strata. Forest temperatures in summer thus increase upwards in amount and range, and the same is true for evaporation and light. The animals of the high bush stratum have not been studied. The stratal occurrence of the animals of the next three strata below is what we should expect if it were due in part at least to physical factors. Thus, a rather large number of species habitually pass between herbs and shrubs and vice versa, while a much smaller number divide their time between the leaf and herb strata. This is of course under summer conditions, and refers to animals which during a given stage of their life cycle habitually divide their activities between the strata in question. This is apparently a temperature response in some cases, such as the downward migration of *Clastopera obtusa* and its return to the shrubs with rising temperatures. The tendency is seen to be for animals to make the traverse only between strata which are separated by moderate gradients.

Above the high bushes, the coniferous forest may possess a layer of low deciduous trees, and above them lies the forest crown itself. The animal population has not been studied. The instrumental observations indicate changes in the same physical factors and in the same direction, as those already mentioned. The sharp gradient falls between the high

bush and low tree strata, with a mean daily evaporation of 14 cc and 19.7 cc respectively.

The hythergraphs indicate that coniferous forest of the climax type, as distinguished from the subclimax stages of its northern or upper montane border, is in general a region of less climatic severity. The effects of climatic factors are modified by the forest cover of climax trees and substratal plant societies. During the spring, summer and fall the animal population falls into stratal societies, which are in agreement with the stratification of physical factors and vegetation. The latter seems to be of obvious importance to the phytophaga, but since even they respond to physical factors by stratum-to-stratum migrations, and since stratification occurs among such animals as spiders, which possess no direct relations with the vegetation, it seems probable that the physical factors are extremely important and perhaps decisive. During the winter the invertebrate life and to some extent the vertebrate life of this forest becomes concentrated in the ground strata, and the community reverts for the time being to a one-stratum society, like the tundra community of its early successional history.

The climax of the entire series which we are discussing is deciduous forest, wherever climatic conditions permit this to replace the conifers. The area where such succession can take place is one of higher mean temperatures than the region of climax coniferous forest. Deciduous forest of elm and maple, as studied by Weese (1924) under summer conditions seems to possess a stratification of measurable physical factors which agrees in all important respects with that found for the coniferous forest, although mean temperatures are distinctly higher throughout the year, the difference being approximately 5°C.

The difference between shrub and herb temperature as contrasted for coniferous and deciduous forest is under 1.5°C, and evaporation from atmometers at the same height and exposure in the two habitats gives even closer comparisons:

	Mean daily evaporation in cc	
	Coniferous forest	Deciduous forest
On ground under vegetation	8.2	7.3
1 m above ground	11.2	11.2
2.5 m above ground	14.	12.4

It will be seen that differences are small or lacking. The whole suggests a general and stratal similarity of the physical factors in the two habitats. It must be remembered that the evaporating power of air is an index of many other physical factors, such as temperature, humidity and air movement.

The stratal societies of animals described by Weese for elm-maple forest appear in decided harmony ecologically with such societies observed

by the writer for coniferous forest. This may be illustrated by comparing lists of equivalent predominants from the summer shrub societies of the two habitats:

Coniferous forest	Deciduous forest
<i>Clastoptera obtusa</i>	<i>Empoasca viridescens</i>
<i>Tetragatha</i> sp.	<i>Tetragatha laboriosa</i>
<i>Graphocephala coccinea</i>	<i>Erythroneura obliqua</i>
<i>Philodromus</i> sp.	<i>Xysticus elegas</i>
<i>Diaphnidia pellucida</i>	<i>Epitrix brevis</i>

It will be seen that while there is no positive identity of species (the writer's *Tetragnathas* were too young for determination to species) there is a decided ecological similarity between the respective dominants, some of which belong to the same family. Even where the animals are widely separated taxonomically, as in the case of *Diaphnidia pellucida* and *Epitrix brevis*, their similar habits, life-histories and relations to the community, justify their consideration as ecologically similar. There are thus no greater differences between the animals of corresponding strata, or between the mores of the prominent species, than might be expected to occur between different associations of the same formation, although most of the species are different.

Certain widely ranging species occur in both habitats; examples are *Phylomycus carolinensis*, *Hahnia agilis*, *Linyphia phrygiana*, *Theridion frondeum*, *Gypona 8-lineata*, *Scaphoideus autontinens*, *Camponotus herculeanus pennsylvanicus*, *Formica fusca* and *Myrmica scabrinoidis schenoki*. Their presence in corresponding strata of both coniferous and deciduous forest indicates that to such animals the local conditions of the biotic association are of major importance; the general climatic conditions of less importance, or none at all within the ranges considered.

The various animal societies in both coniferous and deciduous forest are thus seen to be composed of animals with similar mores, of whatever species, or to phrase it differently, both habitats possess stratal societies composed of animals which are ecologically equivalent. These animals respond in a similar way to the measured stratification of physical factors and to their fluctuations, as well as to the observed stratification of plants. There is some evidence that the comparison between the two habitats is as close for seasonal societies as for stratal ones, but coniferous forest was not studied for this at critical periods. What evidence exists tends in this direction.

It hence appears that ecologically, it is the forest cover, that is, the biotic association as a whole, that is of importance in determining these two animal communities. The nature of the cover, which is in turn dependent on the climate, is a secondary consideration. Stratification of

animal communities is thus seen to be fully developed in the preclimax forest, as soon as the forest cover becomes well established. So far as we have evidence, it agrees in all important particulars with the same phenomenon in climax deciduous forest. The cover of tall trees, with substrata of lower vegetation at different levels, appears to be the determining factor for the presence of a typical forest animal community. The nature of the trees, the character (within the limits discussed) of the climate, are of less value. Given such a biotic complex has been described, it becomes inhabited by a stratified animal community during the warmer portion of the year.

With the advent of autumn in both forest habitats, there is a general change of the distribution of population. Urged by factors which are not fully known, but among which temperature is probably of prime importance, there begins a downward migration of the animals of the upper strata. This may be preceded or accompanied by an inward migration of forest-margin species (Weese). The entire phenomenon has already been discussed, and it will only be said here that it results in the reduction of the forest community, during the winter, to the status of leaf-soil society. What animal activities exist are confined to vertical migrations in the forest-floor, correlated with temperature and moisture fluctuations. In the coniferous forest habitat the cold is usually so sustained and the covering of snow so deep and enduring, that it is doubtful whether any important vertical movements take place. Under the milder conditions prevailing in the deciduous forest formation snow often does not lie through the entire winter, and warm rains may entirely thaw and wet the leaf and soil strata from time to time. Here vertical migrations may assume large proportions, such a warm and rainy period increasing the population of a two-foot quadrat by hundreds of percent. The amount and character of such response seems to be in some cases a species characteristic; thus among several species of collembola and mollusks, certain ones appear definitely for one period and set of conditions, other species at other times and under different conditions. This phenomenon has not, however, received any detailed study.

Many animals pass the winter in the leaf and top-soil strata, where they are solidly frozen in during considerable periods. The present study afforded no evidence of particular mortality among the animals so exposed.

Winter is thus a period when the forest loses its stratification of animals (birds, some mammals and some tree-inhabiting insects excepted). It is a period when the greatest climatic effect is shown in the restriction of the activities of the community and when, as has been shown, biotic interrelationships are of least importance. It might be said that there exists here an analogy between the forest floor in winter and the early

tundra; both are single-stratum communities where climatic effects are marked and restrictive and biotic effects of comparatively low value.

Further studies in the whole community cycle of forest and tundra communities, especially in their response to the annual rhythm, would no doubt throw much light on the problems of ecological distribution. It seems evident that the relations between such distribution and measurable physical factors are less simple than has been supposed, nor do studies of physical factors made in different habitats at the noncritical period of the year yield, in themselves, data which will explain why certain animal communities are found there. Studies of the entire biotic complex of a given habitat involving the collection of quantitative as well as qualitative data on animal populations, are needed and if possible such studies should be carried through one or more annual cycles in the same habitat and locality. It is suggested that alpine conditions, though they present special problems, might furnish a valuable field for such investigation; there the entire period of activity is condensed into a few months, during which all the seasonal societies could be studied, from the time of emergence to that of hibernation.

## CONCLUSIONS

Alpine tundra animal communities in the northern Appalachians, as contrasted with those at higher altitudes, show succession of predominants and mores from associates inhabiting bare rock to those characteristic of northern coniferous forest.

The animal communities of coniferous and deciduous forests have a different taxonomic composition; only 4.5%, all non-predominants, are common to both. Stratal societies are ecologically similar in the two habitats; thus a shrub predominant of coniferous forest, such as the cicadellid *Graphocephala coccinea*, is represented in deciduous forest by species, such as *Erythroneura obliqua*, possessing a similar type of life history. The same is true for the other strata.

The climatic difference between the two habitats are sufficiently marked to affect the biota; the deciduous forest, at 44°N. lat., possesses a mean temperature higher by 4.1°C and a relative humidity lower by 5.5% than those found in the coniferous forest, at 45°N lat.

The physical differences between corresponding strata of coniferous and deciduous forest are insignificant; the evaporating power of air at the same height and exposure is approximately the same for both.

The stratal societies within these two communities are correlated with physical and biotic differences at different levels; their vertical distribution is independent, within the limits considered, of the climatic conditions determining the association as a whole.

Hibernating animals in deciduous forest show by vertical migrations a stratal response to changes in physical conditions; there is no evidence of excessive mortality during hibernation.

Negative evidence in regard to the physical conditions in the coniferous and deciduous forest habitats indicates the importance of investigating life cycles of both species and communities in their relation to annual rhythms, as the most promising method of attacking the problems of ecological distribution.

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Table I  
Soil Data  
Soil samples from Mt. Ktaadn.

Station	Water %	Dry mat- ter, %	Organic and volatile sub- stances in dry matter, %	Ash %	Organ- ic and Vola- tile N %	cc. n/100 Ba(OH) <sub>2</sub> per 10 gms.	Depth of sam- ple	Clay and silt %	Sand %
Alpine Tundra (Grass)	28.22	71.78	28.37	43.41	0.49	1.5	8 in.	36.4	63.6
Alpine Tundra (Heath)	18.36	81.64	61.70	19.94	0.76	0.6	8 in.	22.3	77.7
Krumm- holz	21.14	78.86	58.48	20.38	0.38	1.8	1 ft.	41.0	59.0

100 parts dry matter contain

	Organic and Volatile	Ash	Nitrogen in organic matter	Depth of sample
Alpine Tundra (Grass)	39.6	60.4	1.70	8 in.
Alpine Tundra (Heath)	75.5	24.5	1.23	8 "
Krumm- holz	74.1	24.9	0.65	12 "

Quantity of water in relation to dry matter is probably not significant, for although the samples were kept in tightly corked bottles until analyses could be made, a considerable time elapsed before this could be done.

Table II  
Biotic Data

Mammals Recorded from the Upper Stations of Mount Ktaadn

Common Name	Scientific Name	Author
Red Squirrel.....	<i>Sciurus hudsonicus loquax</i> Bangs*	B. H. D.
White-footed Mouse.....	<i>Peromyscus maniculatus abietorum</i> (Bangs).....	
Porcupine.....	<i>Erethizon dorsatum dorsatum</i> (Linnaeus).....	
(Bog-lemming).....	<i>Synaptomys sphagnicola</i> Preble.....	B. H. D.
Short-tailed Shrew.....	<i>Blarina brevicauda talpoides</i> (Gapper).....	
Red Fox.....	<i>Vulpes fulva</i> (Demarest).....	R. D.

Canada Lynx.....	<i>Lynx canadensis canadensis</i> Kerr.....	P. S.
Red-backed Mouse.....	<i>Eutamias gapperi gapperi</i> (Vigors).....	
Woodchuck.....	<i>Marmota monax monax</i> (Linnaeus).....	R. D.
Varying Hare.....	<i>Lepus americanus virginianus</i> (Harlan).....	B. H. D.
Caribou.....	<i>Rangifer caribou caribou</i> (Gmelin).....	B. H. D.
Shrew.....	<i>Sorex personatus personatus</i> I. Geoffroy.....	B. H. D.
Weasel.....	<i>Mustela cicognanti</i> Bonaparte.....	B. H. D.

The species are listed roughly in order of their occurrence through the succession stages, the animals noted first being those found in the earlier associates. Many of them range through a number of successional stages indifferently. The species given in parentheses is the only one that is not found also on the lower slopes covered with *Picea-Abies* forest (Stations E-2, E).

The authorities given for some of the records are:

B. H. D. = B. H. Dutcher, "Mammals of Mt. Ktaadn, Maine" 1903

P. S. = Percival Sayward, "A Winter Ascent of Mt. Ktaadn," 1915

R. D. = Mr. Roy Dudley, who was Dutcher's guide.

\* The single specimen collected by the writer was referred by Mr. Gerrit S. Miller, Jr., to *Sciurus hudsonicus gymnicus* Bangs.

Table III  
Biotic Data

Mammals Recorded Only From the Lower Station of Mount Ktaadn.		
Common Name	Scientific Name	
Water Shrew.....	<i>Neosorex albibarbis</i> Cope.....	*
Marten.....	<i>Marles americana americana</i> (Turton).....	*
Mink.....	<i>Mustela vison vison</i> Schreber.....	*
Meadow-mouse.....	<i>Microtus pennsylvanicus pennsylvanicus</i> (Ord.)...	*
Jumping-mouse.....	<i>Zapus hudsonius hudsonius</i> (Zimmerman).....	*
Jumping-mouse.....	<i>Napaeozapus insignis insignis</i> (Miller).....	
White-tailed Deer.....	<i>Odocoileus virginianus borealis</i> (Miller).....	
Black Bear.....	<i>Euarctos americanus americanus</i> (Pallas).....	*
Fisher.....	<i>Marles pennanti pennanti</i> (Erzleben).....	*
Moose.....	<i>Alces americana americana</i> (Clinton).....	

The first part of the list contains species which have been recorded from the upper as well as the lower regions of the *Picea-Abies* taiga, especially from Chimney Pond (2,900 feet elevation) and thence up to the foot of the steep slopes; the latter part of the list contains species listed only for the lower slopes of the mountain. None of these animals have been reported from the upper plateau regions.

Mostly (records marked \*) on the authority of Dutcher.

Table IV  
Biotic Data

Birds Recorded from the Upper Stations of Mount Ktaadn

Common Name	Scientific Name	Authority
Ruffed Grouse.....	<i>Bonasa umbellus</i> .....	R. D.
Sharp-shinned Hawk.....	<i>Accipiter velox</i> .....	
Broad-winged Hawk.....	<i>Buteo platypterus</i> (?).....	
Bald Eagle.....	<i>Haliaeetus leucocephalus</i> (?).....	A. H. N.
(Crossbill).....	<i>Loxia curvirostra minor</i> (?).....	A. H. N.
White-throated Sparrow.....	<i>Zonotrichia albicollis</i> .....	
Slate-colored Junco.....	<i>Junco hyemalis</i> .....	
(American pipit).....	<i>Amphisp. rubescens</i> .....	A. H. N.

The species in parentheses are the only ones that have not also been recorded for the lower slopes covered with *Picea-Abies* forest.

The authorities for records not taken by the writer's party are: Mr. Arthur H. Norton, of the Portland Society of Natural History (A. H. N.), and Roy Dudley (R. D.), who was Dutcher's guide in 1902.

Table V  
Biotic Data

Birds Recorded Only From the Lower Stations of Mount Ktaadn

Common Name	Scientific Name	*
Canada Grouse.....	<i>Canachites canadensis canadensis</i> .....	
Red-shouldered Hawk.....	<i>Buteo lineatus lineatus</i> .....	
Hairy Woodpecker.....	<i>Dryobates villosus</i> .....	
Downy Woodpecker.....	<i>Dryobates pubescens</i> .....	
Arctic Three-toed Woodpecker.....	<i>Picoides arcticus</i> .....	*
American " ".....	<i>Picoides americanus</i> .....	
Northern Flicker.....	<i>Colaptes auratus luteus</i> .....	*
Olive-sided Flycatcher.....	<i>Nuttallornis borealis</i> .....	
Bluejay.....	<i>Cyanocitta cristata</i> .....	
Canada Jay.....	<i>Peresoreus canadensis</i> .....	
American Crow.....	<i>Corvus brachyrhynchos</i> .....	
Purple Finch.....	<i>Carpodacus purpureus</i> .....	*
Cedar Waxwing.....	<i>Bombycilla cedrorum</i> .....	
Black-and-white Warbler.....	<i>Mniotilta varia</i> .....	*
Myrtle Warbler.....	<i>Dendroica coronata</i> .....	
Magnolia Warbler.....	<i>Dendroica magnolia</i> .....	
Black-poll Warbler.....	<i>Dendroica striata</i> .....	
Winter Wren.....	<i>Nannus hiemalis</i> .....	
Brown Creeper.....	<i>Certhia familiaris americana</i> .....	*
White-breasted Nuthatch.....	<i>Sitta carolinensis</i> .....	*
Red-breasted Nuthatch.....	<i>Sitta canadensis</i> .....	
Black-capped Chickadee.....	<i>Parus atricapillus</i> .....	
Hudsonian Chickadee.....	<i>Parus hudsonicus littoralis</i> .....	*
Golden-crowned Kinglet.....	<i>Regulus satrapa</i> .....	
Hermit Thrush.....	<i>Hylocichla guttata pallasi</i> .....	
Golden-crowned Kinglet.....	<i>Regulus satrapa</i> .....	
Hermit Thrush.....	<i>Hylocichla gutta pallasi</i> .....	

\* = records furnished by Mr. Arthur H. Norton.

Table VI  
Biotic Data

Amphibians and Reptiles from the Lower Stations of Mount Ktaadn

Common Name	Scientific Name	Remarks
Spotted Salamander.....	<i>Ambystoma maculatum</i> (Shaw).....	Tadpoles
Salamander.....	<i>Eurycea bislineata</i> (Green).....	Adults
Common toad.....	<i>Bufo americanus</i> Holbrook.....	Adults and tadpoles
Green-frog.....	<i>Rana clamitans</i> Latreille.....	"
Wood-frog.....	<i>Rana sylvatica</i> LeC.....	"
Common Garter Snake.....	<i>Thamnopsis sirtalis</i> (L.).....	"

Table VII

## Soil Data

Soil Sample from Coniferous Forest at Orono

Depth of Sample	Water %	Dry Matter %	Organic and volatile substances	Ash %	Organic and vola- tile N, %	Cc. n/100 NaOH per 10 grams	Clay and Silt	Sand
			in dry mat- ter, %				%	
8 in	26.95	73.05	46.25	26.80	1.25	0.7	66.7	33.3

100 parts dry matter contain

	Organic and volatile	Ash	Nitrogen in organic matter
8 in	63.3	36.7	2.71

Quantity of water in relation to dry matter is probably not significant, for although the samples were kept in a tightly covered can until analyses could be made, a considerable time elapsed before this could be done, and some water loss may have taken place.

Table VIII

## Temperature Data

Temperature in ground under dead leaf stratum of coniferous forest.

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Total Range	Mean Range
June 30	15.6	9.4	13.6	11.3	12.4	6.2	2.3
July 7	15.7	10.6	14.0	11.6	13.0	5.1	2.4
July 14	18.3	12.5	16.0	14.7	15.2	5.8	1.3
July 21	15.8	11.4	14.4	11.8	13.5	4.4	2.6
July 28	16.7	11.7	15.6	13.4	13.3	5.0	2.2
*Aug 4	16.7	11.7	15.9	13.3	14.1	5.0	2.6
Aug 11	18.3	10.6	16.9	14.0	15.3	7.7	2.9
Aug 18	18.1	11.7	15.8	13.3	14.6	6.4	2.5
Aug 25	15.6	10.9	13.9	11.7	13.2	4.7	2.2
*Sept 1	17.0	13.9	16.0	14.2	15.2	3.1	2.0

\* Figures based on data for less than seven days

Table IX

## Temperature Data

Temperature in dead leaf stratum on ground in coniferous forest

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Total Range	Mean Range
*July 21	16.1	13.3	15.5	13.3	14.5	2.8	2.2
July 28	17.2	12.2	15.5	13.6	14.5	5.0	1.9
Aug 4	21.1	12.2	16.6	13.3	15.6	8.9	3.3
Aug 11	22.2	12.2	18.0	15.0	16.7	10.0	3.0
Aug 18	17.8	12.2	15.6	13.4	14.5	5.6	2.2
Aug 25	15.6	12.2	14.2	13.1	13.9	3.4	1.1
*Sept. 1	17.0	14.4	16.1	15.0	15.6	2.6	1.1

\* Figures based on data for less than seven days.



Table X

## Temperature Data

Temperature .6 meter above the surface of the ground in coniferous forest

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Total Range	Mean Range
June 16	23.3	0.6	10.6	7.7	8.8	22.7	2.9
June 23	28.4	4.5	21.7	14.9	17.9	23.9	6.8
June 30	29.4	8.9	24.8	13.3	16.2	20.5	11.5
July 7	28.9	7.2	22.9	13.4	17.8	21.7	9.5
July 14	30.0	13.3	24.9	18.3	21.2	16.7	6.6
July 21	27.2	7.8	20.4	14.6	17.1	19.4	5.8
July 28	27.2	7.8	22.8	14.5	19.6	19.4	8.3
*Aug 4	28.1	5.3	22.7	13.2	17.6	22.8	9.5
Aug 11	29.8	5.6	24.7	16.0	20.0	24.2	8.7
Aug 18	23.9	7.0	19.4	12.8	15.7	16.9	6.6
Aug 25	23.3	6.7	18.7	12.2	15.1	16.6	6.5
*Sept 1	26.1	15.0	21.1	16.8	18.6	11.1	4.3

\* Figures based on data for less than seven days

Table XI

## Temperature Data

Temperature 11 meters above the surface of the ground in coniferous forest

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Base Mean	Total Range	Mean Range	Mean Range above Base
June 16	22.2	6.1	19.1	10.3	13.6	11.7	16.1	8.8	6.6
June 23	25.0	6.7	22.8	10.0	15.4	12.5	18.3	12.8	9.2
June 30	27.8	10.0	22.1	12.5	16.8	14.4	17.8	9.6	6.5
July 7	27.3	9.4	24.1	13.3	17.0	13.9	17.9	10.8	10.1
July 14	27.8	13.9	25.4	16.1	20.5	18.2	13.9	9.3	7.2
July 21	26.7	10.0	21.7	13.4	17.2	15.3	16.7	8.3	6.5
July 28	27.8	10.0	25.5	13.9	18.5	16.3	17.8	11.6	9.6
Aug 4	28.3	7.8	24.8	12.0	18.1	15.5	20.5	12.8	9.3
Aug 11	30.6	12.2	27.9	16.8	21.1	17.9	18.4	11.1	8.7
Aug 18	22.8	7.2	21.7	11.6	15.2	13.9	15.6	10.1	7.8
Aug 25	22.8	8.3	20.6	12.2	15.9	13.4	14.5	8.4	7.1
*Sept 1	26.7	16.1	23.2	16.7	18.9	17.8	10.6	6.5	5.3

\* Figures based on data for less than seven days

Table XII

## Humidity Data

Relative humidity .6 meter above the surface of the ground in coniferous forest

Week ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean R. H.	Total Range	Mean Range
June 16	100.0	31.0			77.4	69.0	
June 23	96.0	44.0	81.8	65.2	73.5	52.0	16.6
June 30	100.0	45.0	93.1	76.0	84.5	45.0	17.1
July 7	98.0	56.0	83.7	75.0	92.5	42.0	8.7
July 14	100.0	38.0	89.4	77.5	84.9	62.0	11.9
July 21	100.0	36.0	83.0	69.8	76.4	64.0	13.2

July 28	100.0	45.0	96.7	74.2	85.4	55.0	22.2
*Aug 4	98.0	40.0	90.5	68.0	79.2	58.0	22.5
Aug 11	100.0	48.0	85.8	62.8	74.4	52.0	23.0
Aug 18	100.0	44.0	99.0	71.1	85.0	56.0	27.9
Aug 25	100.0	49.0	94.2	74.4	84.3	51.0	19.8
*Sept 1	100.0	58.0			90.7	42.0	17.0

\* Figures based on data for less than seven days

Table XIII

## Humidity Data

Relative humidity 11 meters above the surface of the ground in coniferous forest

Week ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean R. H.	Base Mean	Total Range	Mean Range	Mean Range below Base
June 16	82.0	31.0	74.1	44.6	62.5	65.6	51.0	29.5	20.4
*June 23	95.5	30.0	92.9	35.6	71.3	65.5	65.5	57.3	23.9
June 30	100.0	27.0	89.4	49.7	69.7	79.3	73.0	39.7	29.1
July 7	99.0	31.5	98.8	41.7	74.2	93.4	67.5	57.1	51.6
July 14	100.0	23.0	94.9	48.1	74.2	82.5	77.0	37.8	34.4
July 21	100.0	27.0	77.2	27.0	72.6	86.2	73.0	50.2	40.0
July 28	100.0	33.0	98.6	46.0	75.7	87.3	67.0	52.6	41.4
Aug 4	100.0	22.0	97.6	37.0	73.1	85.4	78.0	60.6	40.7
Aug 11	100.0	34.0	97.6	44.3	77.9	87.3	66.0	53.3	42.9
Aug 18	100.0	31.0	99.0	55.3	84.8	96.2	69.0	43.7	40.2
Aug 25	100.0	26.0	98.6	56.3	81.0	92.3	74.0	42.3	36.3
*Sept 1	100.0	41.0	95.0	63.8	81.8	92.6	59.0	31.2	27.8

\* Figures based on data for less than seven days

Table XIV

## Evaporation Data from Pine Forest, Obtained with Porous Cup Atmometers

Sta No	1	2	3	4	5	6	7	8	9
Height (M)	1.0	1.0	0.3	2.5		0.3	6.5	11.0	0.3
Date (wk.)	Average daily evaporation in cc. (reduced to standard)								
June 23	*	*	*	*	*	*	*	*	
June 30	10.4	9.5	7.2	12.5	0.9	5.4	17.7	18.8	
July 7		12.3	10.0	16.9	0.4	† 6.9	21.8	23.7	*
July 14		14.3	12.1	19.6	0.2		27.0	27.2	18.5
July 21	*	13.7	9.6	18.9	0.3		25.5	26.8	18.8
July 28	14.4	13.6	11.7	18.4	0.3		23.8	26.4	16.2
Aug 4		15.4	*	19.2	0.3		25.1	26.8	15.8
Aug 11		7.8	4.4	10.2	0.04		13.0	13.1	†
Aug 18		6.0	4.3	8.1	0.03		10.5	10.6	
Aug 25		7.5	5.0	10.1	0.04		14.6	15.4	

\* The date on which a given atmometer was placed in position, and marks the beginning of the evaporation which was recorded one week later.

† This instrument was moved on July 7 to Station No. 9

‡ This instrument was destroyed, and no further observations were taken at the station

Table XIVa

## Location of Stations

- 1 Black atmometer sphere, exposed on specially constructed stand 2 meters from instrument shelter
- 2 White atmometer sphere, exposed with No. 1
- 3 White atmometer sphere, on ground under shrubs, near Nos. 1 and 2
- 4 White atmometer sphere, suspended from lower branch of small hemlock
- 5 White atmometer sphere, placed in an observation cavity dug in the soil, and covered with a grating on which was placed the usual layer of pine needles and other forest floor debris; the sphere was just beneath this mat
- 6 White atmometer sphere, on ground in swampy glade; long grass
- 7 White atmometer sphere, in pine tree
- 8 White atmometer sphere, at level of upper branches
- 9 White atmometer sphere, on ground at western forest margin, among shrubs and weeds, but exposed to wind over short grass area

Table XV

Summer Variations in Light Intensity in Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924

*On the Ground*

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:11 P M	80.0	Sun shining through light clouds
Aug 7	2:17 P M	60.0	Clear
Aug 8	2:00 P M	67.0	Clear
Aug 8	2:12 P M	158.0	Sun shining through light clouds
Aug 10	2:09 P M	170.0	Fair; sun shining through light clouds
Aug 11	2:01 P M	180.0	Clear; sun shining through light clouds
Aug 12	2:48 P M	487.5	Cloudy; very dull and raining
Aug 13	1:20 P M	125.0	Fair
Aug 15	1:16 P M	235.0	Clear; diffused light
Aug 16	2:09 P M	281.0	Diffused light
Aug 17	1:46 P M	271.0	Diffused light shining through clouds
Aug 18	1:06 P M	175.0	Fair; sun shining through light clouds
Aug 19	3:22 P M	2100.0	Very dull; raining heavily
Aug 21	2:25 P M	354.5	Dull
Aug 22	1:58 P M	515.0	Very dull
Aug 23	1:44 P M	470.0	Cloudy and dull
Aug 25	2:21 P M	570.0	Cloudy and very dull
Aug 27	2:53 P M	461.0	Cloudy

Table XVI

Summer Variations in Light Intensity in Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924

*1.5 meters above Ground*

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:14 P M	33.0	Sun shining through light clouds
Aug 7	2:19 P M	14.5	Clear

Aug 8	2:03 P M	39.0	Clear
Aug 8	2:15 P M	127.5	Sun shining through light clouds
Aug 10	2:13 P M	147.0	Fair; sun shining through light clouds
Aug 11	2:05 P M	162.0	Clear; sun shining through light clouds
Aug 12	2:48 P M	240.0	Cloudy; very dull and raining
Aug 13	1:25 P M	83.0	Fair
Aug 15	1:19 P M	94.0	Clear; diffused light
Aug 16	2:12 P M	89.0	Diffused light
Aug 17	1:51 P M	196.0	Diffused light shining through clouds
Aug 18	1:10 P M	143.0	Fair; sun shining through light clouds
Aug 19	3:32 P M	420.0	Very dull; raining heavily
Aug 21	2:37 P M	211.5	Dull
Aug 22	2:02 P M	220.0	Very dull
Aug 23	1:48 P M	114.0	Cloudy and dull
Aug 25	2:31 P M	420.0	Cloudy and very dull
Aug 27	2:09 P M	90.0	Cloudy

Table XVII

Summer Variations in Light Intensity in Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924  
In Open Glade

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:20 P M	15.0	Sun shining through light clouds
Aug 7	2:23 P M	12.0	Clear
Aug 8	2:06 P M	16.0	Clear
Aug 8	2:18 P M	47.0	Sun shining through light clouds
Aug 10	2:17 P M	25.0	Fair; sun shining through light clouds
Aug 11	2:21 P M	30.0	Clear; sun shining through light clouds
Aug 12	2:52 P M	90.0	Cloudy; very dull and raining
Aug 13	1:28 P M	30.0	Fair
Aug 15	1:23 P M	56.0	Clear; diffused light
Aug 16	2:15 P M	65.0	Diffused light
Aug 17	1:55 P M	39.0	Diffused light shining through clouds
Aug 18	1:12 P M	45.0	Fair; sun shining through light clouds
Aug 19	3:37 P M	90.0	Very dull; raining heavily
Aug 21	2:40 P M	47.0	Dull
Aug 22	2:02 P M	61.0	Very dull
Aug 23	1:48 P M	33.0	Cloudy and dull
Aug 25	2:50 P M	83.0	Cloudy and very dull
Aug 27	2:21 P M	37.0	Cloudy

Table XVIII

Summer Variations in Light Intensity in Grassland Adjoining Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924  
On the Ground

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:27 P M	4.0	Sun shining through light clouds
Aug 7	2:28 P M	3.0	Clear
Aug 8	2:09 P M	3.0	Clear

Aug 8	2:21 P M	3.0	Sun shining through light clouds
Aug 10	2:20 P M	8.0	Fair; sun shining through light clouds
Aug 11	2:24 P M	10.0	Clear; sun shining through light clouds
Aug 12	2:57 P M	13.0	Cloudy; very dull and raining
Aug 13	1:32 P M	6.5	Fair
Aug 15	1:26 P M	7.0	Clear; diffused light
Aug 16	2:17 P M	20.0	Diffused light
Aug 17	1:58 P M	10.0	Diffused light shining through clouds
Aug 18	1:15 P M	9.0	Fair; sun shining through light clouds
Aug 19	3:40 P M	15.0	Very dull; raining heavily
Aug 21	2:42 P M	5.0	Dull
Aug 22	2:07 P M	9.0	Very dull
Aug 23	1:54 P M	10.0	Cloudy and dull
Aug 25	2:53 P M	15.0	Cloudy and very dull
Aug 27	2:23 P M	6.0	Cloudy

Table XIX

## Biotic Data

Animal population of coniferous forest, considered by strata and as a whole,

July 7 to Sept. 1, 1924

Date	Soil Coll	Str Ave	Leaf Coll	Str Ave	Herb Coll	Str Ave	Shrub Coll	Str Ave	Total	Per Acre (Thousands)	Per Hectare
Jul 7	1	18	1	9	1	44	1	32	103	1,121	3,039
Jul 21	2	13	2	37	2	14	2	26	90	980	2,656
Jul 28	2	5	2	8	2	95	2	18	126	1,426	3,864
Aug 11	1	16	1	15	1	23	1	42	96	1,045	2,831
Aug 14	1	11	1	21	1	30	1	14	76	827	2,241
Aug 18	1	17	1	34	1	34	1	33	118	1,285	3,482
Aug 21	1	8	2	44	1	15	1	16	83	903	2,447
Aug 25	1	6	1	11	1	79	3	44	140	1,524	4,130
Sept 1	1	4	1	21	1	40	1	41	106	1,154	3,127

Table XX

## Biotic Data

Animal population of deciduous forest, considered by strata and as a whole,

October 6, 1924, to March 2, 1925

Week ending	Soil Coll	Str Ave	Leaf Coll	Str Ave	Herb Coll	Str Ave	Shrub Coll	Str Ave	Total	Per Acre (Thousands)	Per Hectare
Oct 6	2	16	3	81	3	28	3	46	183	1,992	5,400
Oct 13	1	68	1	42	1	77	1	41	228	2,482	6,728
Oct 27	1	10	1	48	1	24	1	27	109	1,187	3,216
Nov 3	1	48	2	59	1	7	1	13	127	1,383	3,748
Nov 10	1	11	1	124	1	34	1	5	174	1,894	5,135
Nov 17	1	10	1	74	1	14	1	2	100	1,089	2,951
Nov 24	1	37	1	196	1	7	1	1	241	2,624	7,112
Dec 1	1	20	2	87	1	1	1	0	108	1,176	3,187
Dec 8	1	21	1	165	1	8	1	4	198	2,156	5,843
Dec 22	1	18	1	15	1	0	1	0	33	359	973
Dec 29	1	37	1	28	1	0	1	0	65	707	1,203

Jan 5	1	26	1	78	1	0	1	0	104	1,132	3,059
Jan 12	1	20	1	25	1	0	1	0	45	490	1,328
Jan 19	1	28	1	53	1	0	1	0	81	882	2,388
Jan 26	1	15	1	37	1	0	1	0	52	571	1,549
Feb 2	1	24	1	64	1	0	1	0	88	958	2,597
Feb 9	1	9	1	331	1	0	1	1	343	3,735	10,122
Feb 16	1	23	1	131	1	1	1	0	155	1,687	4,574
Feb 23	1	37	1	260	1	6	1	1	304	3,310	8,971
Mar 2	1	30	1	1	1	0	1	0	31	337	914

Table XXI

## Winter Bird Census of Cottonwood (January 5-March 2, 1925)

The forest margin is characterized by presence of thick growths of bushes and is adjacent on three sides to fields of corn. The interior is characterized, throughout the greater part of its extent, by absence both of bushes dense enough to afford shelter and of low branching trees.

In the third column of the following lists M indicates *forest margin*; I indicates *interior*.

Species are listed in order of abundance

## I. Species Always Present

Name	Estimated Number	Location	Stratum	Remarks
Slate-colored junco ( <i>Junco hyemalis</i> )	15	M(I)	Bushes, ground; trees rarely	In flocks, often with tree sparrows
Tree Sparrow <i>Spizella monticola</i>	10	M	Bushes, ground	In flocks of juncos
Tufted titmouse ( <i>Baeolophus bicolor</i> )	8	I(M)	Tree tops, bushes rarely	Often in flocks of 3 to 5
Blue jay ( <i>Cyanocitta cristata</i> )	5	I(M)	Trees oftenest, bushes, ground	Very conspicuous, often in flight
Northern flicker ( <i>Colaptes auratus luteus</i> )	5	I,M	Trees	Often in flight
Cardinal ( <i>Cardinalis cardinalis</i> )	5♂2	I,M	Trees, bushes	
Downy woodpecker ( <i>Dryobates pubescens medius</i> )	♀3			
	3♂1	I,M	Trees	
Hairy woodpecker ( <i>Dryobates villosus</i> )	2♂1	I,M	Trees	
Red-bellied woodpecker ( <i>Centurus carolinus</i> )	1	I	Trees	Conspicuous, until last week of Jan. Not seen later

Table XXII

## Biotic Data

## Winter Bird Census of Cottonwood

The individuals of the first two species listed doubtless changed from day to day, as flocks of juncos and tree sparrows were seen frequently crossing the fields to and from the forest. The numbers of column two represent an estimate of the number of individuals

which could practically always be found by hunting throughout approximately the same parts of the forest. The numbers given are based on the daily records but are an estimate, inasmuch as it was never possible, on one day, to study all parts of the forest with equal thoroughness; also it was difficult to be absolutely certain, in the case of such birds as the titmice and the blue jays, how much allowance to make for "repeaters" in the day's record.

The first three species listed appeared occasionally in much larger flocks. Blue jays and northern flickers were more numerous than the census indicates on a few warm days in February, when they formed small flocks (each with its own species).

Name	Species Frequently Present			Remarks
	Estimated Number	Location	Stratum	
American crow ( <i>Corvus brachyrhynchos</i> )	5	I	Above trees	In flight
Chickadee ( <i>Parus atricapillus</i> )	2	M(I)	Bushes, trees	With juncos, usually at margin
Hawks (probably <i>Buteo</i> , at least 2 species)	1	M,I	Above and between trees (Trees)	In flight usually, tree-tops rarely

Table XXIII

Biotic Data  
Winter Bird Census of Cottonwood  
Species Occasionally Present

Name	Estimated Number	Location.	Stratum	Remarks
Bob-white ( <i>Colinus virginianus</i> )	6	I	Ground	Under fallen, leafy trees. Only in very cold weather
Mourning dove ( <i>Zenaidura macroura carolinensis</i> )	4	M	Ground, low branches	Once only
English sparrow ( <i>Passer domesticus</i> )	4	M	Tree	Once only, though abundant at farmyard opposite
Redpoll ( <i>Acanthis linaria linaria</i> )	2 ♀	M	Bushes, ground	Once only in flock with juncos and tree sparrows. (Probably more common.)
Goldfinch ( <i>Astragalinus tristis</i> )	10	M	Above trees	In flight, across edge of forest. Once only
Golden crowned kinglet ( <i>Regulus satrapa</i> )	1	I	Ground	Once only
Migrant shrike ( <i>Lanius ludovicianus</i> ) (var. <i>migrans</i> )	1	M	Tree	Once only
Bronzed grackle ( <i>Quiscalus quiscula aeneus</i> )	1		Above trees	In flight across forest. Once only
White-breasted nuthatch ( <i>Sitta carolinensis</i> )	1			Once only heard

Table XXIV  
Biotic Data  
Winter Bird Census of Cottonwood  
Spring Migrants

Name	Estimated Number	Location	Stratum	Earliest Date	Remarks
Robin ( <i>Planesticus migratorius</i> )	2 to 25	I,M	Trees, ground; above trees	Feb 16	The larger number in flocks. Often in flight
Rusty blackbird ( <i>Euphagus carolinus</i> )	6 to 18 (♀ 2)	I,M	Trees, bushes, ground	Feb 27	In flocks
Red-winged blackbird ( <i>Agelaius phoeniceus</i> )	1 or 2	M	Trees, bushes	Mar 2	With flocks of rusty blackbirds
Bluebird ( <i>Sialia sialis</i> )				Feb 8	Once only in forest until after three weeks of cold weather with which winter study closed.

Some of the birds of the list above, instead of being strictly migrants, may have been individuals which had wintered in this latitude in sheltered retreats from which they appeared on favorable days. A few also were probably early summer residents, as in the case of the robins who, after their first appearance, were always present to the number of two or three in the forest.

## XXV

## Biotic Data

## Winter Birds of Cottonwood, January, 1925

The following list states the number of individuals of each species seen on the date given.

January	5	12	19	21	23	24	26	29	31
Quail ( <i>Colinus virginianus</i> ) . . . . .	—	—	—	—	6 or 8	—	—	—	—
Mourning Dove ( <i>Zenaidura</i> ) . . . . .	—	—	—	—	—	—	—	—	4
Hawk (large) . . . . .	—	1	2	—	1	—	—	1	1
( <i>Buteo borealis</i> )									
( <i>Buteo lineatus</i> ) probably both									
Hairy woodpecker ( <i>Dryobates villosus</i> ) . . . . .	—	—	—	—	—	1 ♀	1	—	1
Downy woodpecker ( <i>Dryobates pubescens medianus</i> ) . . . . .	—	—	3	—	2	2	1	1	—
Red-bellied woodpecker ( <i>Centurus carolinus</i> ) . . . . .	1	—	1	1	1	—	—	—	—
Flicker ( <i>Colaptes auratus luteus</i> ) . . . . .	—	—	4	6	4	1	—	—	5
Blue jay ( <i>Cyanocitta cristata</i> ) . . . . .	3	3	4	3	2	2	2	3	3
Crow ( <i>Corvus brachyrhynchos</i> ) . . . . .	2	—	3	5	—	—	5	9	7
Bronzed Grackle ( <i>Quiscalus quiscula aeneus</i> ) . . . . .	—	—	1	—	—	—	—	—	—
Tree sparrow ( <i>Spizella monticola</i> ) . . . . .	—	—	—	10	10	—	—	—	2
Junco ( <i>Junco hyemalis</i> ) . . . . .	—	—	15	5	—	—	—	—	5
Cardinal ( <i>Cardinalis cardinalis</i> ) . . . . .	—	1	3 ♀	1 ♀	2 (1 ♀)	—	—	—	3 (1 ♀)



Migrant shrike ( <i>Lanius ludovicianus migrans</i> ).....	—	—	—	—	—	1	—	—	—
Tufted titmouse ( <i>Baeolophus bicolor</i> )	4	—	4	5	3	8	3	5	2
Chickadee ( <i>Penthestes atricapillus</i> )..	1	—	—	—	—	—	—	—	—
Golden-crowned kinglet ( <i>Regulus satrapa</i> ).....	1	—	—	—	—	—	—	—	—
English sparrow ( <i>Passer domesticus</i> )..	—	—	—	—	—	—	—	4	—

## Birds of Cottonwood, February 2 to March 2 (Inclusive)

The following list states the number of individuals of each species estimated to be present on the given date.

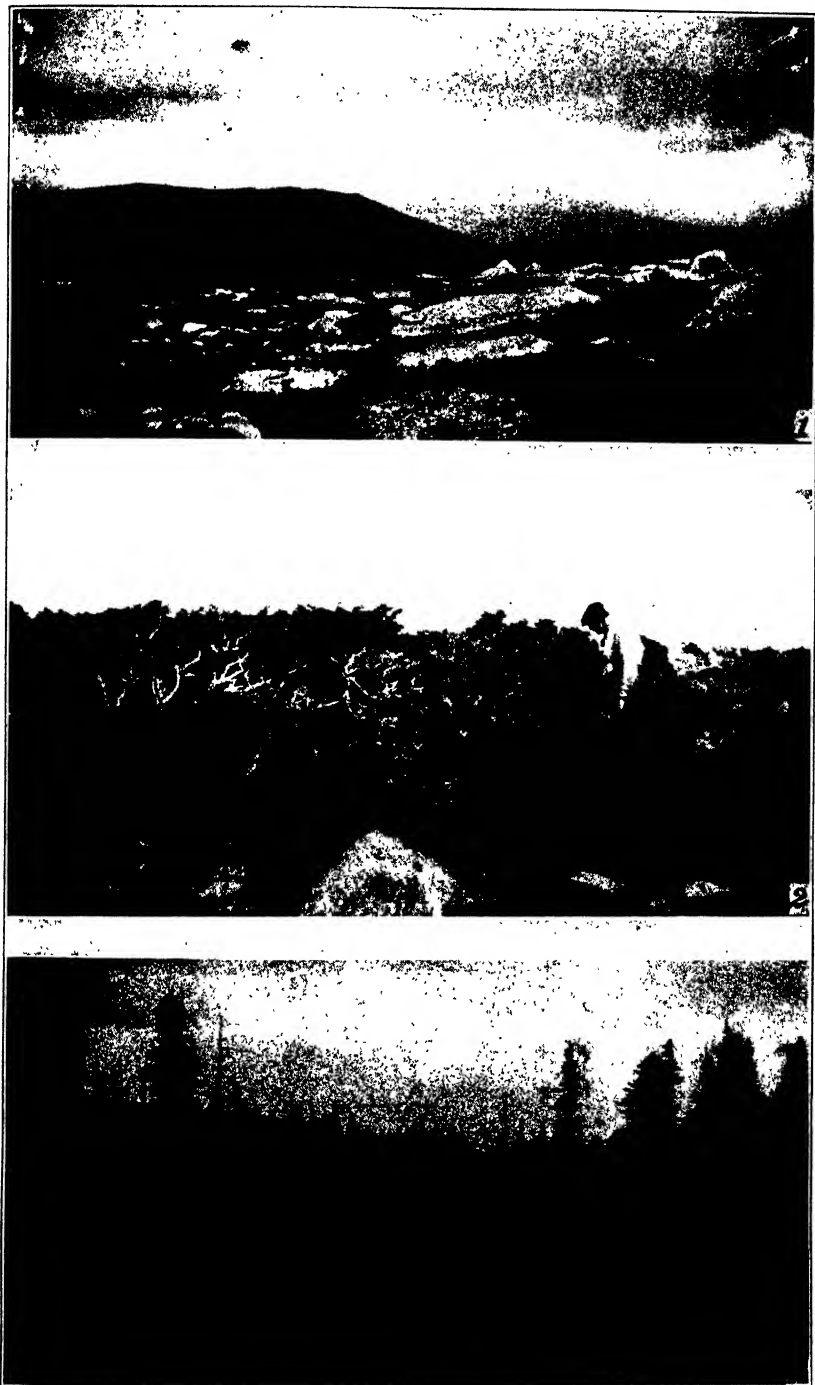
	F2	6	8	9	13	16	23	27	M2
Hawk (large) ( <i>Buteo</i> sp.).....	1	—	1	—	—	—	—	1	1 or 2
Hairy woodpecker ( <i>Dryobates villosus</i> ).....	—	—	—	1	1♂	1	—	—	—
Downy woodpecker ( <i>Dryobates pubescens medianus</i> ).....	2♂	—	—	1	3♂	1♂	3♂	—	2♂
Flicker ( <i>Colaptes auratus luteus</i> )... 8	3	—	—	6	5	1	—	1	—
Blue jay ( <i>Cyanocitta cristata</i> )..... 5	3	—	—	7	3	4	4	5	5
Crow ( <i>Corvus brachyrhynchos</i> )....	—	5	—	4	9	3	6	2	4
Red-winged blackbird ( <i>Agelaius phoeniceus</i> ).....	—	—	—	—	—	—	—	—	1 or 2
Rusty blackbird ( <i>Euphagus carolinus</i> ).....	—	—	—	—	—	—	—	18	6♀
Redpoll ( <i>Acanthis linaria linaria</i> )..	—	—	—	—	—	—	2♀	—	—
Goldfinch ( <i>Astragalinus tristis</i> )....	—	—	—	—	—	—	—	—	10
Tree sparrow ( <i>Spizella monticola</i> ).. 10	—	—	—	—	—	—	20	—	3
Slate-colored junco ( <i>Junco hyemalis</i> ).....	52	10	—	20	10	8	10	10	18
Cardinal ( <i>Cardinalis cardinalis</i> )... 2	5	3♀	—	—	—	—	2	1♀	2
White-breasted nuthatch ( <i>Sitta carolinensis</i> ).....	—	—	1(heard only)	—	—	—	—	—	—
Tufted titmouse ( <i>Baeolophus bicolor</i> ).....	7	5	—	20	6	8	12	9	3
Chickadee ( <i>Penthestes stricapillus</i> )..	—	—	—	2	2	—	—	2	2
Robin ( <i>Planesticus migratorius</i> )....	—	—	—	—	—	2	3	15	26
Bluebird ( <i>Sialia sialis</i> ).....	—	—	—	—	—	—	—	—	—

1(Species report only)

**PLATE I**

## EXPLANATION OF PLATE I

1. Station C, at an elevation of 5,080 feet on the Table-land of Mount Ktaadn. The characteristic vegetation consists of various grasses and sedges.
2. Station D. Krummholz.
3. Station F. Pond-bog habitat; Pamola Pond, 2,700 feet elevation.





**PLATE II**

## EXPLANATION OF PLATE II

4. Interior of coniferous forest at Orono, Maine, showing the exposure of instruments. The instrument shelter contained a thermograph and a hygrograph, which were thus raised to a height of 11 m above the surface of the ground. An atmometer may be seen in a bracket on the shelter and another hanging from the shelter, 6 m above the ground.
5. The deciduous forest habitat at Urbana, Illinois, as it appeared during much of the winter study.







**PLATE III**

**EXPLANATION OF PLATE III****Map of Upper Regions of Mount Ktaadn**

(After sketch map by Parker B. Field, published by the Appalachian Mountain Club.)

**Fig. 6. Ecological stations as follows:**

**Station A—Rock Animal Community**

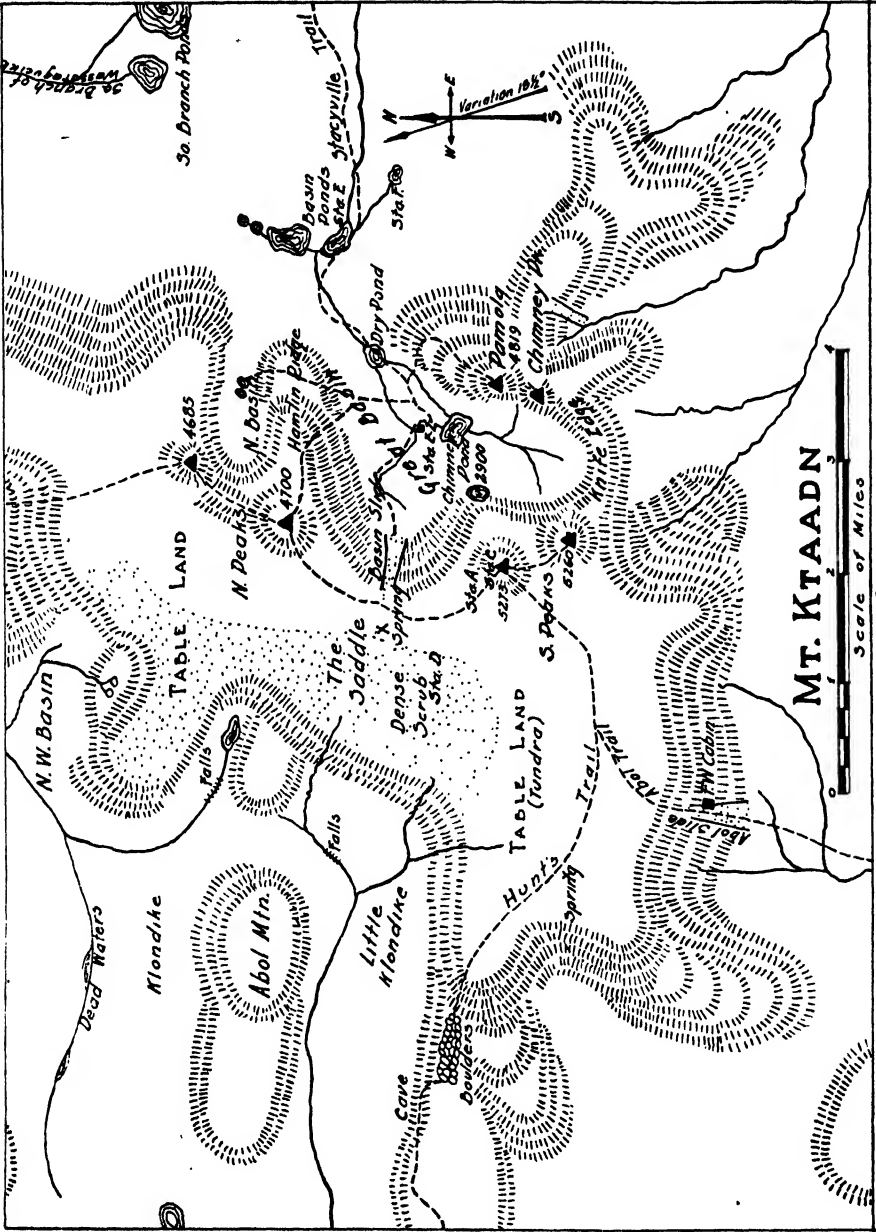
**Station C—Tundra Animal Community**

**Station D—Krummholz Animal Community**

**Station E-2—Upper Climax Forest Animal Community**

**Station E—Lower Climax Forest Animal Community**

**Station F—Pond-bog Animal Community.**



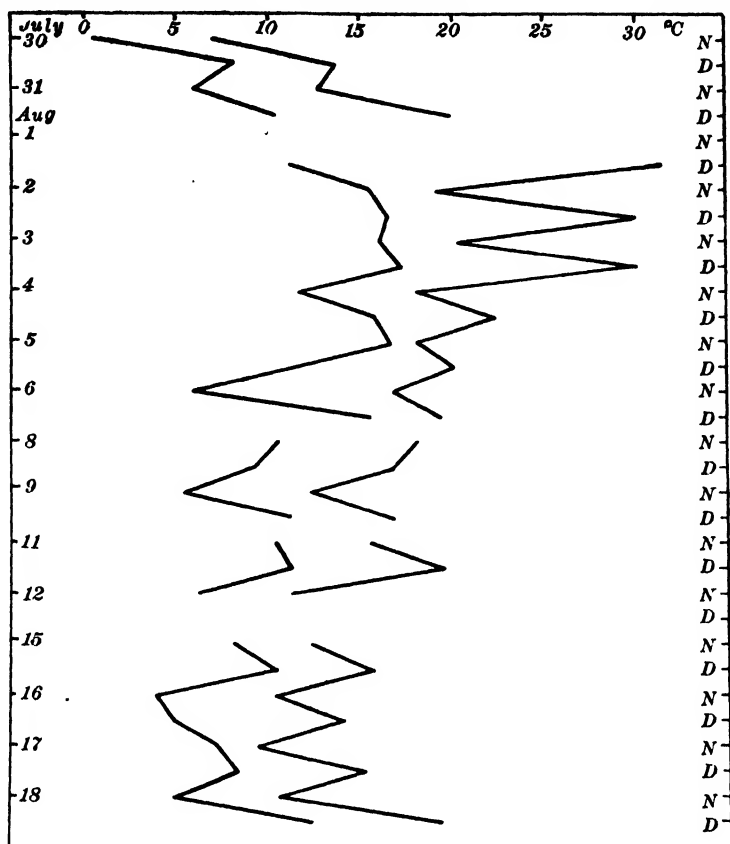


## PLATE IV

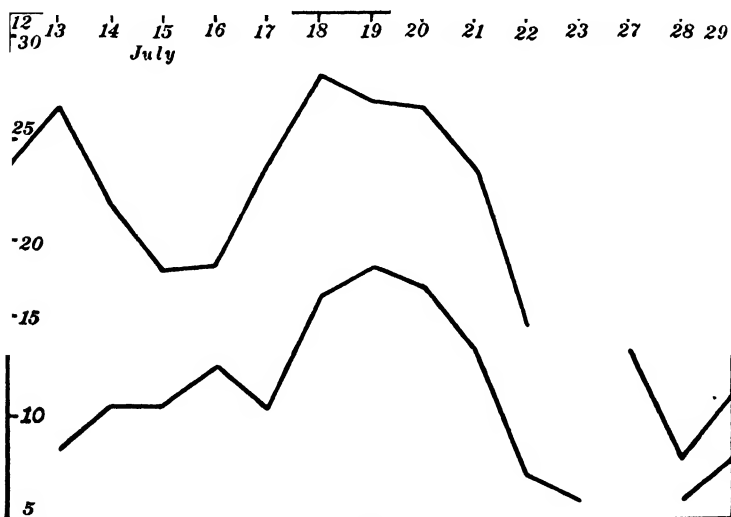
## EXPLANATION OF PLATE IV

7. Maximum and minimum temperatures at Chinney Pond on Mt. Ktaadn. D=day, N=night.
8. Maximum and minimum daily temperatures at Basin Pond on Mount Ktaadn.
9. Hythergraphs of localities under consideration.

The horizontal scale shows precipitation in inches, the vertical temperature in degrees Centigrade. The broken curve represents the conditions of precipitation and temperature at Ft. Chimo, Ungava. The graph which is ruled horizontally is for Orona, Maine. That which is ruled vertically is for Mt. Washington, New Hampshire.



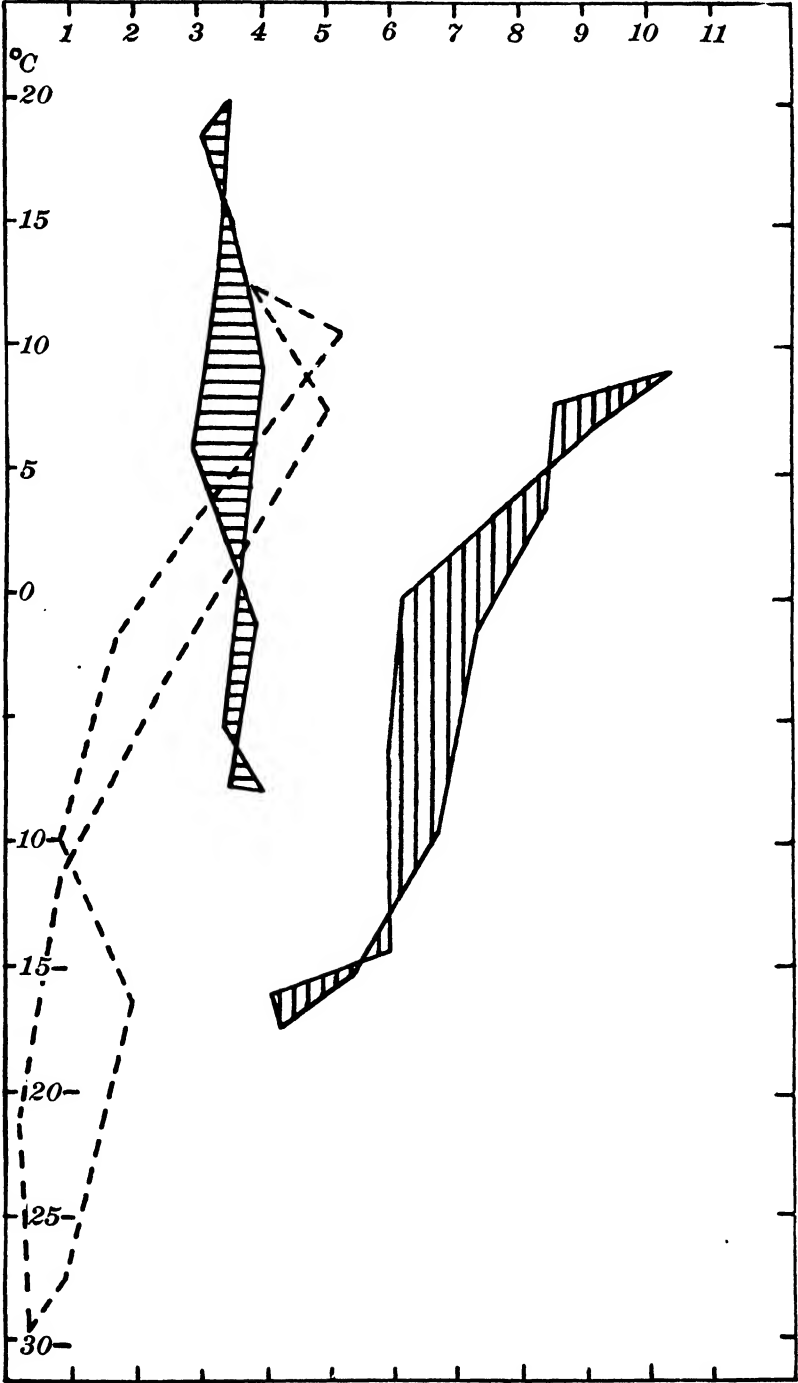
7



8









## PLATE V

## EXPLANATION OF PLATE V

10. Weekly mean temperatures at various strata of the coniferous forest habitat.

A=Temperature 0.6 m above the ground.

B=Temperature 11 m above the ground.

C=Temperature in the ground, under the mat of dead leaves.

D=Temperature in the mat of dead leaves.

All temperatures are centigrade degrees, with a base at 10°, and horizontal rulings at 15°, 20° and 25°, respectively. Each Centigrade degree is indicated by smaller divisions on the lateral margins.

The mean temperatures for the weeks ending June 16, 23, and 30, July 7, 14, 21 and 28, August 4, 11, 18 and 25, and September 1, are indicated by the labels and divisions at the upper and lower margins. The records for some of the strata were not begun until the study had been progressing some time.

11. Weekly mean variations of temperatures at various strata of the coniferous forest habitat.

A=Variation in temperature 0.6 m above ground.

B=Variation in temperature 11 m above ground.

C=Variation in temperature in ground, under dead leaf stratum.

D=Variation in temperature in dead leaf stratum.

Notations similar to those used in 1. The base-line is at 0°C; horizontal rulings indicate 5°, 10° and 15°C.

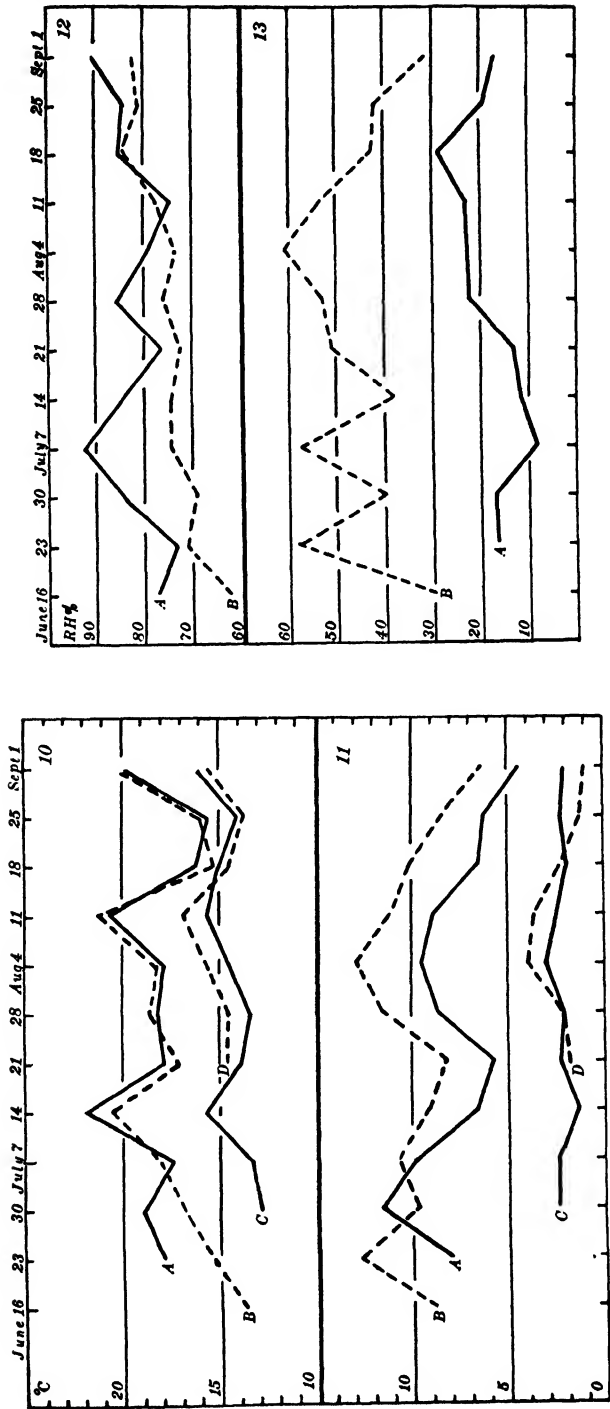
## Humidity Data

12. Weekly mean relative humidity at two levels in the coniferous forest habitat: 0.6 m (A) and 11 m (B) above the ground.

Divisions on the upper and lower margins indicate the weekly intervals. Horizontal rulings are placed at each 10% of relative humidity, with a base-line drawn at 60% and the top line representing 100% relative humidity.

13. Weekly mean variations in relative humidity at two levels in the coniferous forest habitat: 0.6 (A) and 11 m (B) above ground.

The base-line is 0% relative humidity, and the horizontal lines above stand for additional increments of 10% relative humidity up to 70%.





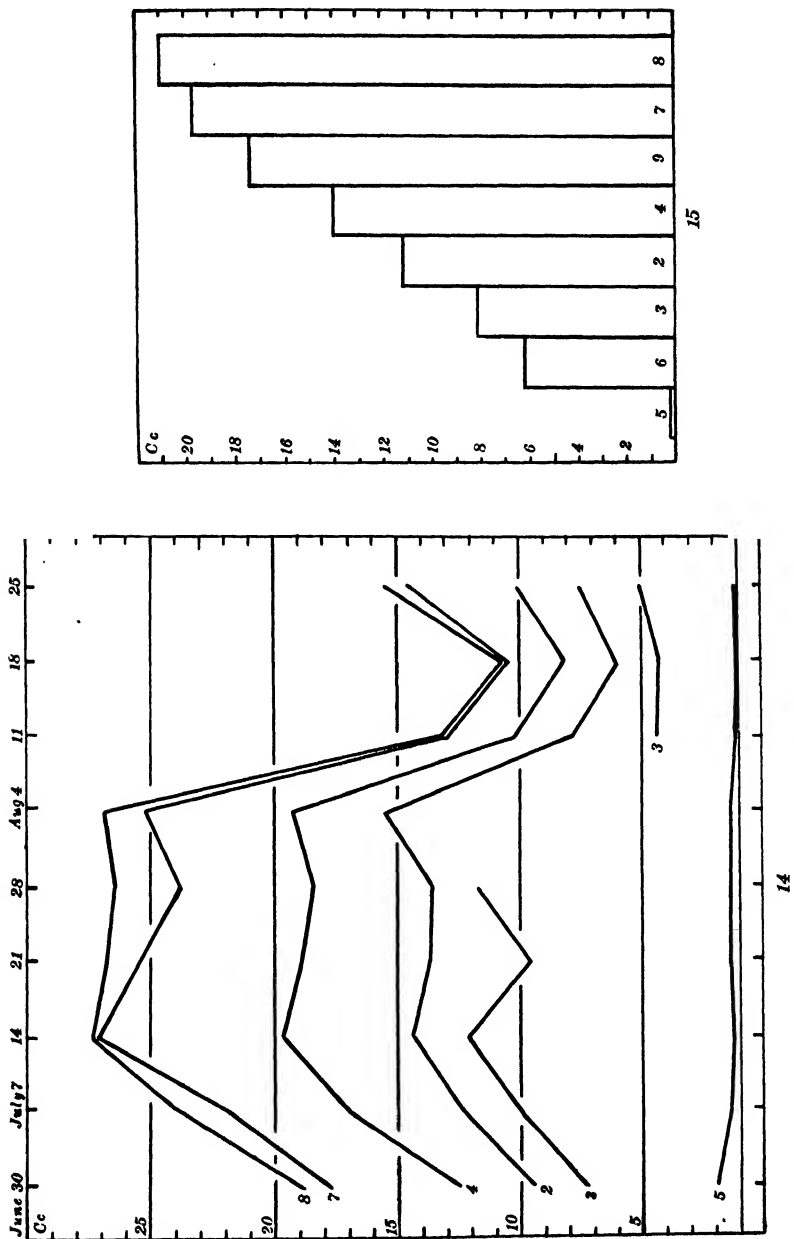
**PLATE VI**



## EXPLANATION OF PLATE VI

## Evaporation Data from Pine Forest

14. Evaporation from porous cup atmometers at stations 2, 3, 4, 5, 7 and 8, in mean Daily Evaporation per week.  
The vertical scale is divided into increments of 1 cc, with horizontal lines drawn at 5, 10, 15, 20 and 25 cc. The vertical scale is divided according to weeks. Each curve is numbered according to the station where it was recorded.
15. Diagram showing the comparative amount of evaporation, in terms of the daily mean, spherical porous cup atmometers at eight stations (No. 2 to No. 9) in the habitat. The data covers the Nine Week Period.  
The scale is divided into vertical increments, showing a range of evaporation of from 0 cc to 21 cc, expressed in terms of the daily mean for the period of study, each division representing 1 cc. The columns represent the various stations, to correspond with which they are numbered.





## PLATE VII

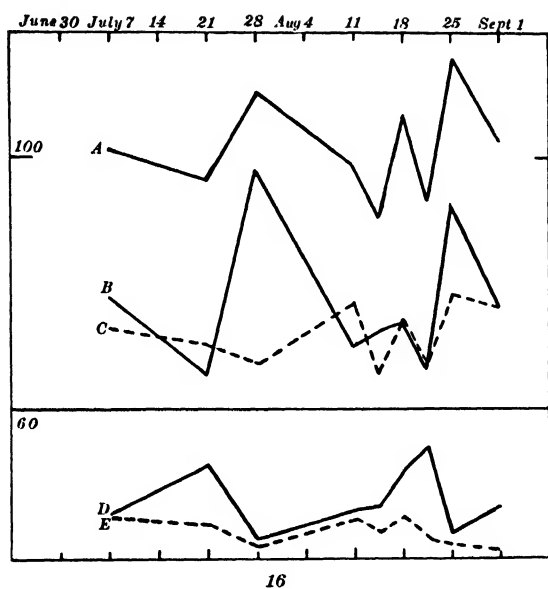
## EXPLANATION OF PLATE VII

## Biotic Data

16. Animal population, as a whole and according to strata, in coniferous forest, July 7 to September 1, 1914.

The divisions along the upper and lower margins represent the weeks, as in the plates on temperature and humidity. The divisions along the lateral margin indicate ten animals taken in collecting.

A—Total population; B—Population of herb stratum; C—Population of shrub stratum; D—Population of leaf stratum; E—Population of soil stratum.





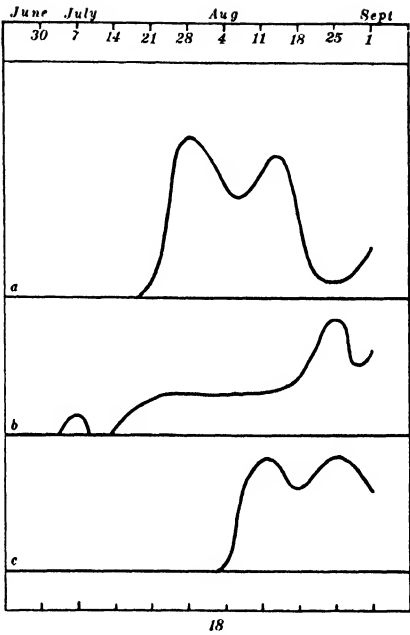
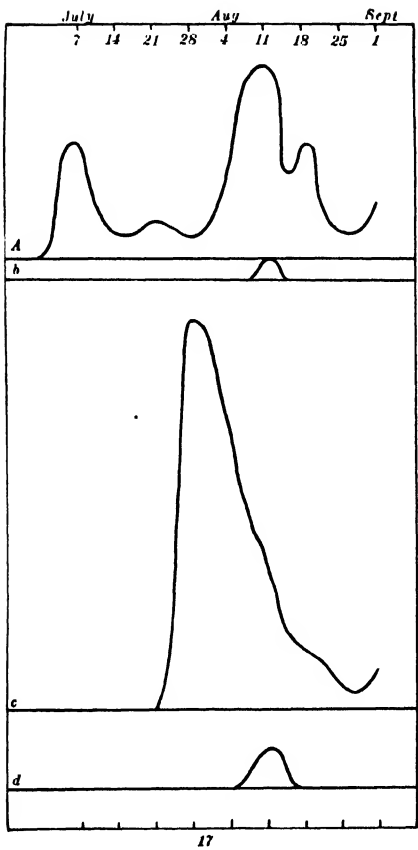
## PLATE VIII



## EXPLANATION OF PLATE VIII

## Resident Population of the Lowest Strata

17. Resident population of the lowest strata
  - A. *Helodrilus caliginosus* trapezoides (Dugès)
  - B. *Tomocerus flavescens* Tullberg var. *separatus* Folsom.
    - b. Herb stratum
    - c. Leaf stratum
    - d. Soil stratum
18. Summer Population of Arachnida
  - a. *Leiobunum politum* Weed.
  - b. *Linyphia* sp. (juvenile)
  - c. *Tetragnatha* sp. (juvenile)





## PLATE IX

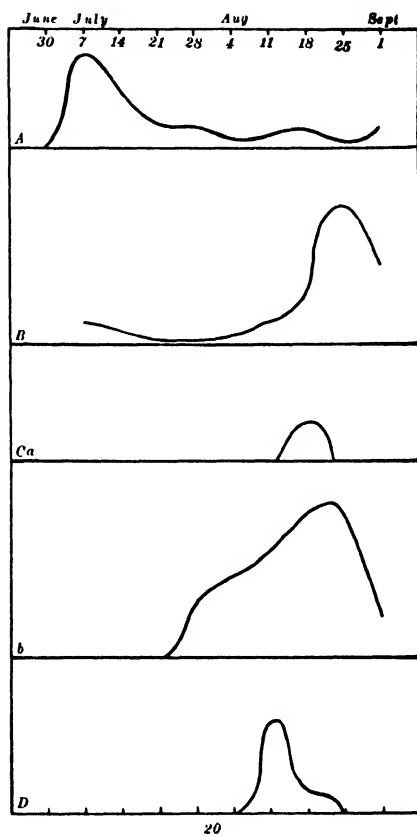
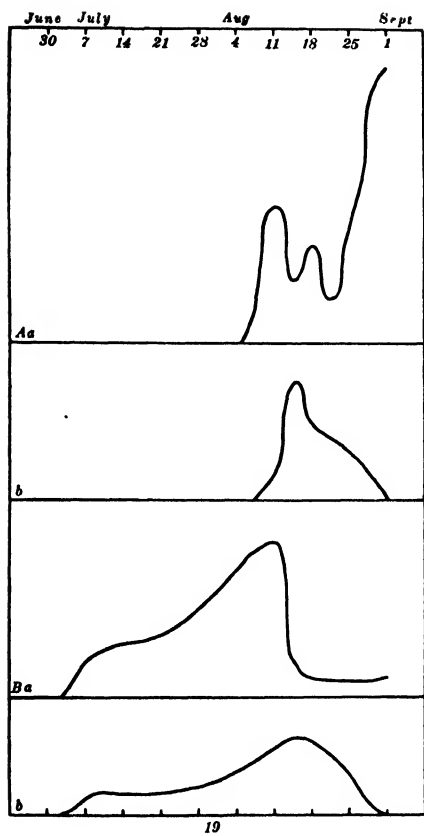
## EXPLANATION OF PLATE IX

## 19. Summer Population of Homoptera

- A *Clastoptera obtusa* (Say)
  - a. Shrub stratum
  - b. Herb stratum
- B *Graphocephala coccinea* (Forst.)
  - a. Shrub stratum
  - b. Herb stratum

## 20. Summer and Stratal Populations of Homoptera and Hemiptera

- A *Macrosiphum coryli* Davis
- B *Nabis* sp. (juvenile)
- C *Dicyphus famelicus* (Uhl.)
  - a. Shrub
  - b. Herb
- D *Diaphnidia pellucida* Uhl.



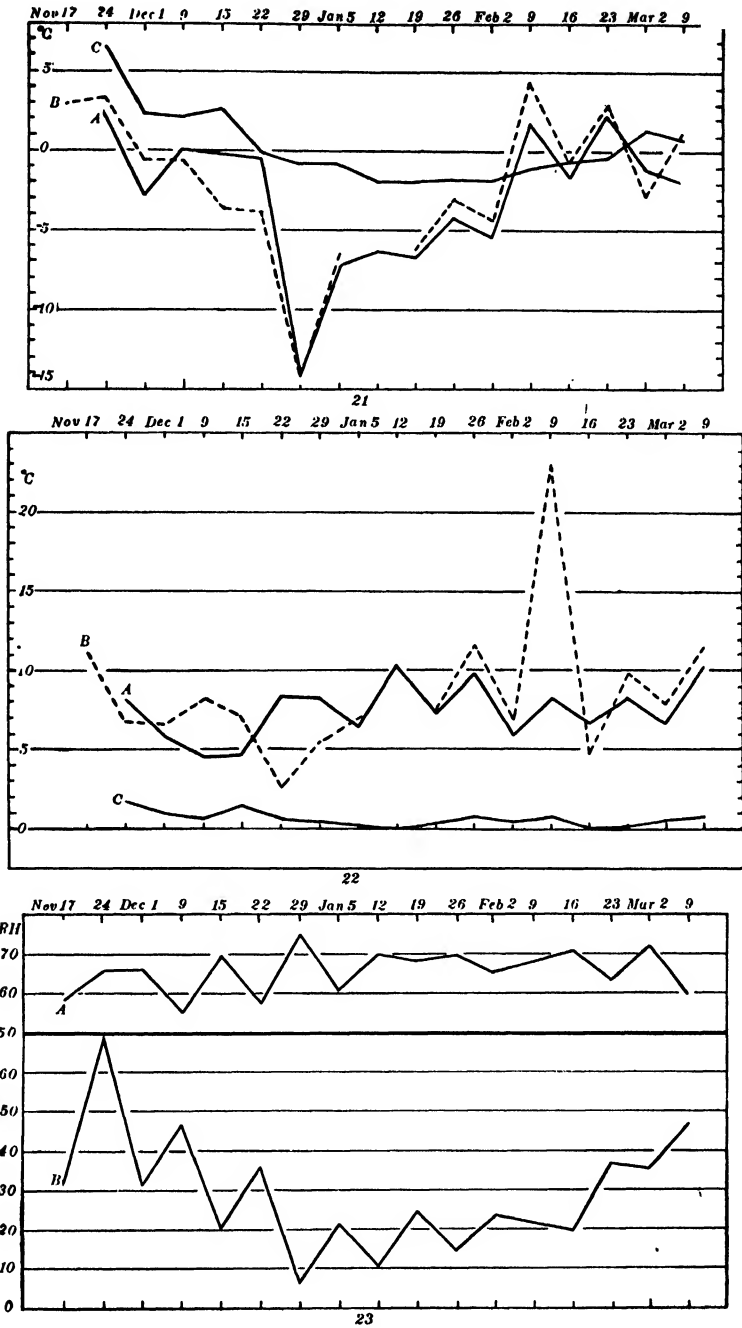


## PLATE X



## EXPLANATION OF PLATE X

21. Weekly mean temperatures at various strata of the deciduous forest habitat: 15 cm below the surface of the ground, 0.6 m and 11 m above the surface.  
All temperatures are Centigrade degrees, with a base at  $-15^{\circ}$ , and horizontal rulings at  $-10^{\circ}$ ,  $-5^{\circ}$ ,  $0^{\circ}$ ,  $5^{\circ}$ ,  $10^{\circ}$ , respectively. Each Centigrade degree is indicated by smaller divisions on the margins.  
The mean temperatures for the weeks ending November 17 and 24, December 1, 8, 15, 22 and 29, January 5, 12, 19 and 26, February 2, 9, 16 and 23, and March 2 and 9, are indicated by the labels and divisions on the longer margins. A break of one week, that of January 12, occurs in the record taken at a height of 11 m.  
A = Temperature .6 m above ground.  
B = Temperature 11 m above ground.  
C = Temperature 15 cm below ground.
22. Weekly mean variations of temperatures at various strata of the deciduous forest habitat: 15 cm below the surface of the ground, 0.6 m and 11 m above the surface. Scheme of representation same as in preceding plate. The base-line is at  $0^{\circ}\text{C}$ .; horizontal rulings indicate  $5^{\circ}$ ,  $10^{\circ}$ ,  $15^{\circ}$ ,  $20^{\circ}$  and  $25^{\circ}\text{C}$ .  
A = Variation in temperature .6 m above ground.  
B = Variation in temperature 11 m above ground.  
C = Variation in temperature 15 cm below ground.
23. Weekly mean relative humidity and weekly mean variations in relative humidity 0.6 m above ground in the deciduous forest habitat.  
Divisions on the upper and lower margins indicate the weekly intervals. Horizontal rulings are placed at each 10% relative humidity, with base-lines drawn at 40% for the weekly mean relative humidity, and at 0% for the weekly mean variations in relative humidity.  
A = Weekly mean relative humidity  
B = Weekly mean variations in relative humidity.



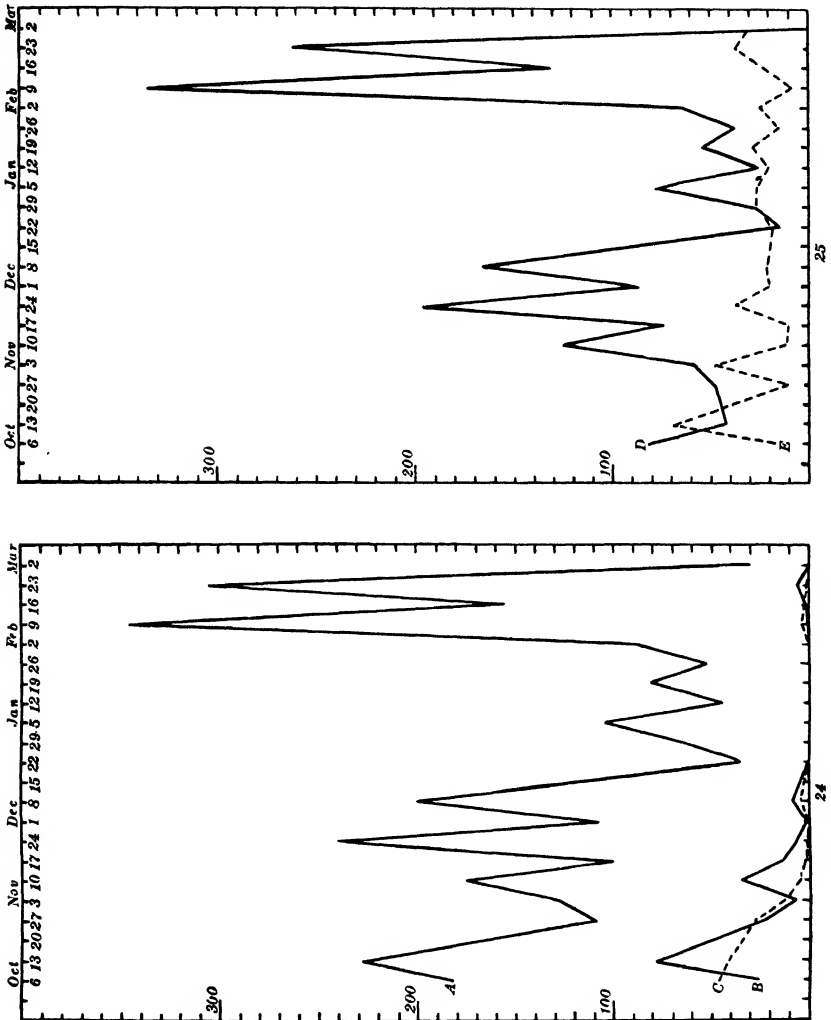


## PLATE XI

## EXPLANATION OF PLATE XI

## Biotic Data

24. Animal population, as a whole and by the two upper strata considered, in deciduous forest, October 6, 1924, to March 2, 1925.  
The divisions along the upper and lower margins represent the weeks, as indicated.  
The divisions along the lateral margins represent ten animals taken in collecting.  
A=Total population.  
B=Population of herb stratum.  
C=Population of shrub stratum.
25. Animal population of the two lower strata deciduous forest, October 6, 1924, to March 2, 1925.  
The divisions along the upper and lower margins represent the weeks, as indicated.  
The divisions along the lateral margins represent ten animals taken in collecting.  
D=Population of leaf stratum.  
E=Population of soil stratum.





## PLATE XII



## EXPLANATION OF PLATE XII

## 26. Winter Populations of Spiders and Mollusks

A *Linyphia phrygiana* C. KochB *Dictyna volupis* Keyserlinga. } Shrub and herb strata  
b. }

c. Leaf stratum

C *Anyphaena rubra* Emer. (juvenile)

a. Shrub stratum

b. Herb stratum

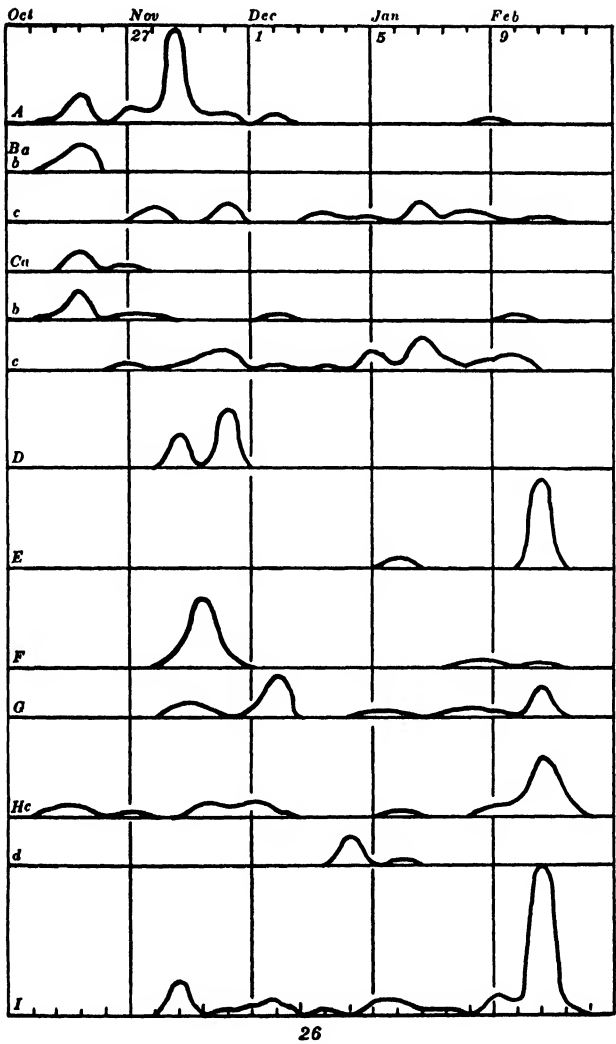
c. Leaf stratum

D *Carychium exile* H. C. LeaE *Zonitoides arborea* (Say)F *Gastrocopta tappaniana* (C. B. Adams)G *Zonitoides minuscula* (Binney)H *Vitrea indentata* (Say)

c. Leaf stratum

d. Soil stratum

I *Carychium exiguum* (Say)

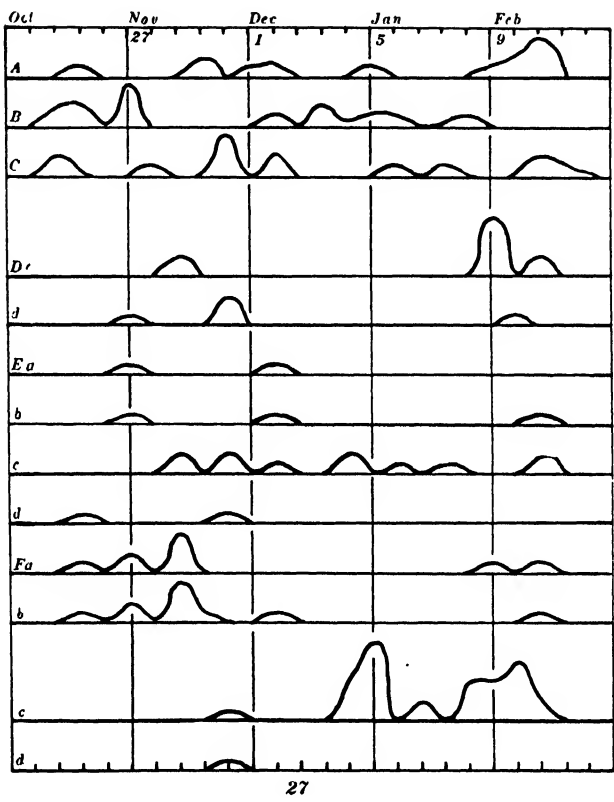




## PLATE XIII

## EXPLANATION OF PLATE XIII

27. Winter Populations of Various Insects.
- A *Cantharis* sp. (larva)
  - B *Meracantha contracta* (Beauv.) (larva)
  - C *Phyllotreta sinuata* (Steph.)
  - D *Tipula* sp. (larva)
    - c. Leaf stratum
    - d. Soil stratum
  - E *Nabis fesus* (L.)
    - a. Shrub stratum
    - b. Herb stratum
    - c. Leaf stratum
    - d. Soil stratum
  - F *Lygus pratensis oblineatus* (Say)
    - a. Shrub stratum
    - b. Herb stratum
    - c. Leaf stratum
    - d. Soil stratum





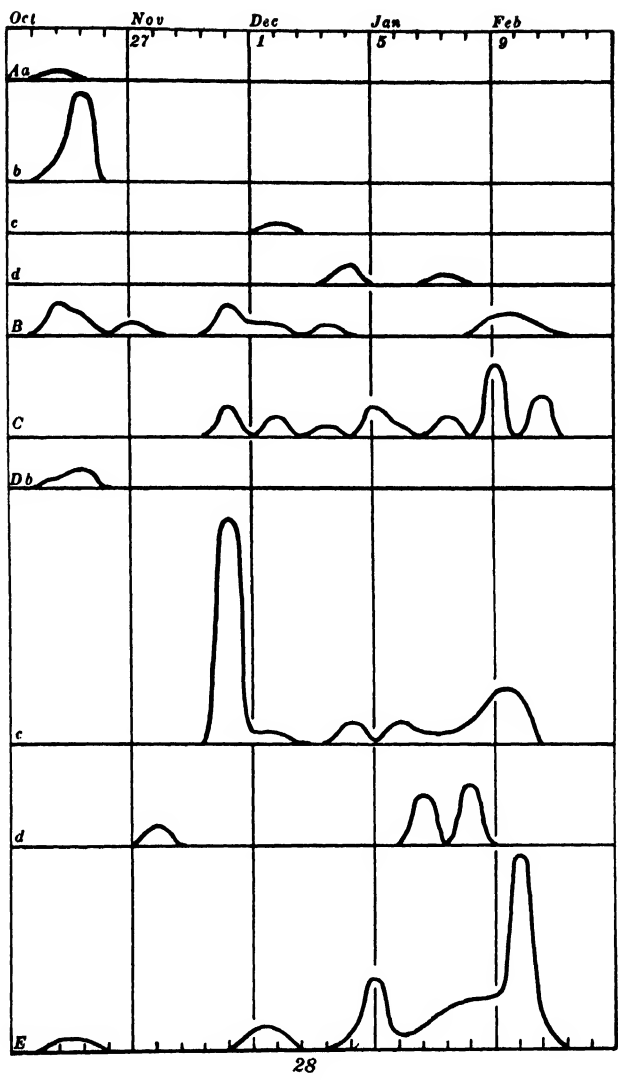
## PLATE XIV



## EXPLANATION OF PLATE XIV .

## 28. Winter Populations of Beetles

- A *Epitrix brevis* Sz.
  - a. Shrub stratum
  - b. Herb stratum
  - c. Leaf stratum
  - d. Soil stratum
- B *Ptilodactyla serricollis* (Say)
- C *Nitidula rufipes* (L.)
- D *Telephanus velox* Hald.
  - b. Herb stratum
  - c. Leaf stratum
  - d. Soil stratum
- E *Malthodes* sp. (larva)





## PLATE XV

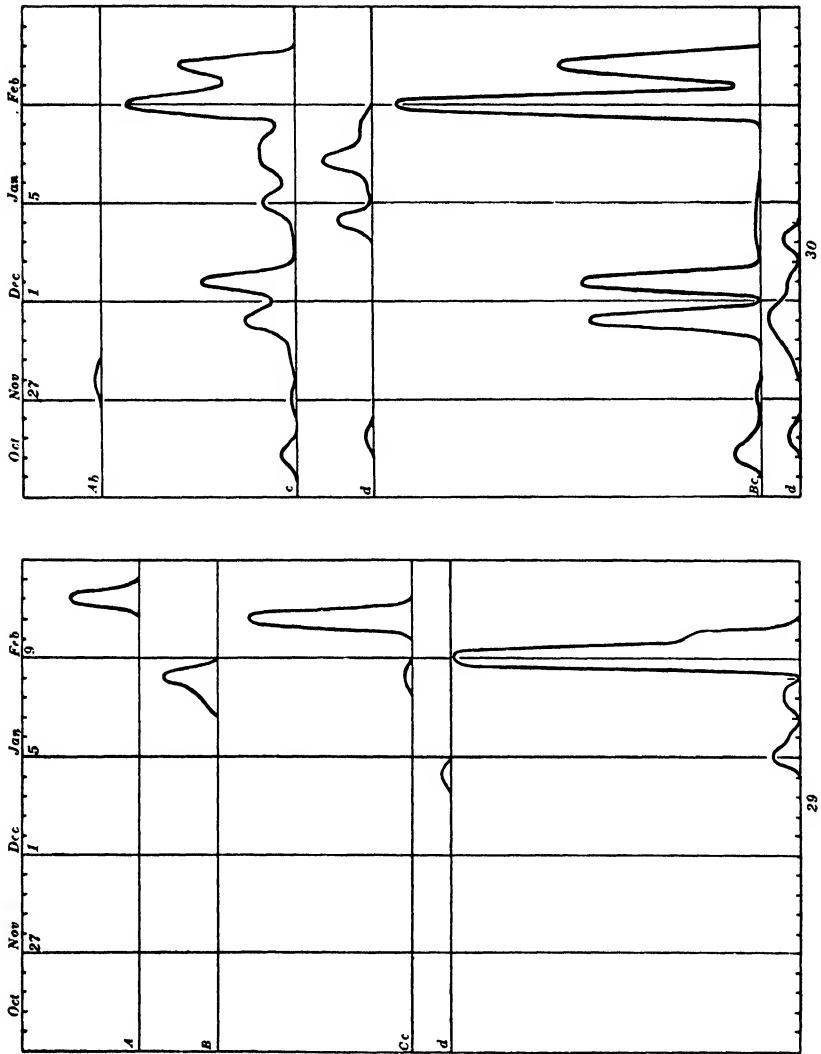
## EXPLANATION OF PLATE XV

## 29. Winter Population of Collembola

- A *Onychiurus fimetarius* (L.)
- B *Onychiurus armatus* Tullberg
- C *Isotoma* sp.
  - c. Leaf stratum
  - d. Soil stratum
- D *Onychiurus subtenuis* Folsom.

## 30. Winter Populations of Collembola and Enchytraeidae

- A *Tomocerus flavescens* Tullberg var. *americanus* Schott
  - b. Herb stratum
  - c. Leaf stratum
  - d. Soil stratum
- B *Enchytraeidae*
  - c. Leaf stratum
  - d. Soil stratum





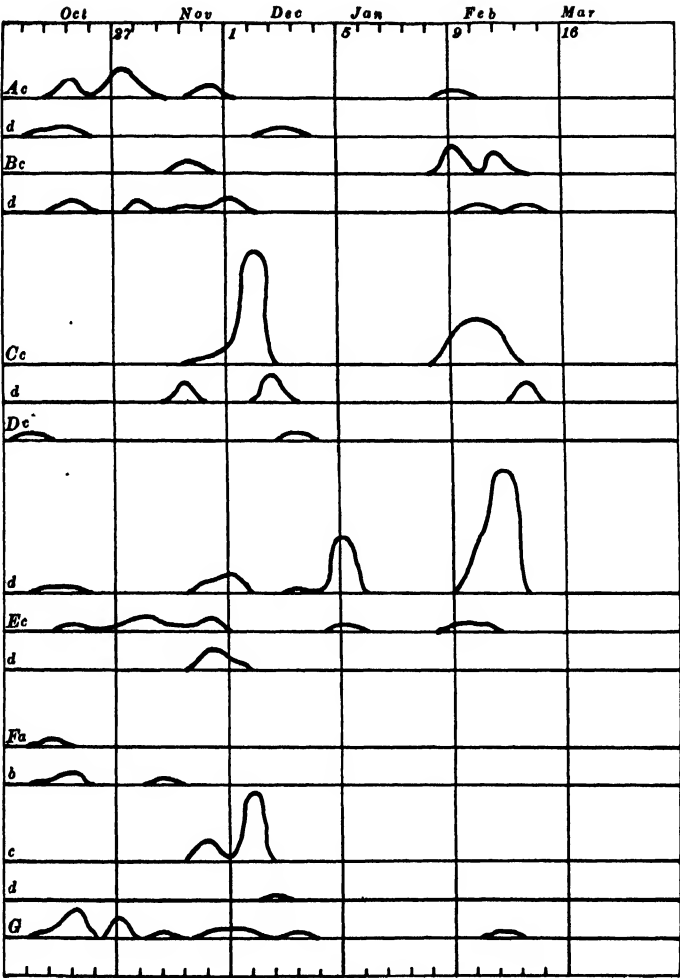
## PLATE XVI



## EXPLANATION OF PLATE XVI

## 31. Winter Populations of Myriapods and Diptera

- A *Linotaenia chionophila* (Wood)
  - c. Leaf stratum
  - d. Soil stratum
- B *Pohobius bilabiatu*s (Wood)
  - c. Leaf stratum
  - d. Soil stratum
- C *Cleiogona caesiannulata* (Wood)
  - c. Leaf stratum
  - d. Soil stratum
- D *Fontaria virginien*sis Dru
  - c. Leaf stratum
  - d. Soil stratum
- E *Scytonotus granulat*us (Say)
  - c. Leaf stratum
  - d. Soil stratum
- F *Leptocera* sp.
  - a. Shrub stratum
  - b. Herb stratum
  - c. Leaf stratum
  - d. Soil stratum
- G *Fannia* sp. (juvenile)





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